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A BEHAVIOURAL ANALYSIS OF COMMUNICATION AMONG FRANKLIN'S GROUSE DURING THE BREEDING SEASON

by

© DENNIS PATRICK NUGENT

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE

DEPT. OF ZOOLOGY

EDMONTON, ALBERTA

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FACULTY OF GRADUATE STUDIES AND RESEARCH

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Supervisor

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Date.....Jan 25.....1979.....

Abstract

Behavioural aspects of the communication system of territorial Franklin's Grouse, Canachites canadensis franklinii, were investigated during the spring and summer of 1976 and 1977, in the foothills of southwestern Alberta. Emphasis was placed on determining how and when these grouse communicate their location to conspecifics in the dense forests that they inhabit, and what role communication may have in maintaining the dispersion of a population throughout appropriate habitat.

Prolonged observations of marked grouse in their natural habitat indicated that both male and female territorial residents advertized their occupation of a space by wing-produced acoustic signals . This advertizing tended to be least frequent around mid-day throughout spring and the mating season among males, and most frequent during dawn and dusk just before and during laying by females. During these periods, females also occasionally advertized with a Cantus during twilight. These vocal signals were additionally used by resident females during threat interactions with female territorial intruders and adjacent resident females. Resident territorial male threat behaviour directed towards other males involved vocal signals and stereotyped displays.

Territorial exclusion was apparently maintained by mutual intrasexual avoidance of areas occupied by other advertizing birds and by threat behaviour during close range

interactions with trespassers.

Territorial behaviour appeared to cease among males and broodless females following the mating period. Advertizing and interactions involving threat behaviour were no longer evident during observations of one or more grouse during this period.

The relevance of the findings to population regulation was considered in a final discussion.

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INTRODUCTION AND RATIONALE

Adult and some yearling Franklin's Grouse occupy relatively exclusive territories during spring (MacDonald 1968; Herzog and Boag 1978). Recent studies of this species have suggested that social behaviour may determine the number of breeding birds that establish territories (Keppie 1975; Herzog and Boag 1978). However, the means by which territories are established and defended are poorly understood, particularly among females. The relatively dense forest habitat (McCourt 1969; McLachlin 1970), low population density (Keppie 1975), cryptic markings, and secretive nature of these grouse have made them relatively difficult to study in the wild. Consequently, studies of individual behaviour in this race have been confined largely to captive birds (Alway 1977), and in the wild, to the conspicuously displaying males in spring (Stoneberg 1967; MacDonald 1968; McLachlin 1970; Hjorth 1970).

Behaviour is the means by which animals are socially organized, allowing the available ecological resources to be shared among them (McBride 1976). An understanding of social organization requires a systematic study of social behaviour (op.cit.). Animal behaviour is basically comprised of movements that are often ordered into sequences which perform functional and communicative operations (op.cit.). Communication includes any signal given by one individual that elicits a response in another (Scott 1968). It follows therefore, that an understanding of how birds communicate

may increase the understanding of the role of social behaviour in regulating the size of the breeding population.

There are two fundamental approaches to studies of behaviour - experimental and observational. Both have different advantages and disadvantages. Many studies of communication in birds have used dummies or recording-playbacks in the fieldwork (Weeden and Falls, 1959; Harju 1969; Beer 1970; Hjorth 1970; Mossop 1971; Emlen 1972; Hannon 1978; to name a few). Although this method ensures some results, a major restriction on studies of animal communication stems from the predominantly stochastic nature of much of this behaviour (Klopfer and Hatch 1968).

Details of minimally distorted behaviour can be observed during close and continued contact with animals free in their natural habitat (Eibl-Eibesfeldt 1970). Only within the kind of environment in which it evolved can the full range of a species behaviour be expected, and its adaptiveness revealed (Smith 1977). Studies of communication can be directed towards the situations in which animals produce signals, the signals themselves, or the response to such signals (Klopfer and Hatch 1968). Repeated observation of signals given in their natural spatial and temporal context may provide useful information on all of these aspects as suggested by Scott (1968:29):

> The study of communication in any animal species should begin with observation of behaviour under natural or semi-natural conditions in order to get some idea of the significance and importance of communication and also to assess the general range of capabilities of the species. Furthermore,

> observation generates ideas in a way that experiments under highly controlled conditions do not. The function of experimentation is to test and refine theories, but major theories themselves originate from careful observation and systematic classification of the data so assembled.

Consequently, in this study I used an observational approach, focussing upon the behavioural patterns of Franklin's Grouse in the wild at the time when they were reported to show marked territoriality (Herzog and Boag 1977, 1978). Specifically, I investigated when and how each sex communicates its location in the forest to conspecifics, and how this communication may affect the spacing of individuals throughout appropriate habitat. This study therefore, is a contribution to the ethogram of Franklin's Grouse.

My findings are presented in the form of two papers:

1. Communication among female Franklin's Grouse during the breeding season.
2. A quantitative analysis of advertizing and intrasexual threat behaviour by territorial male Franklin's Grouse.

The relevance of the findings to population regulation is considered in the final discussion.

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PAPER 1. COMMUNICATION AMONG FEMALE FRANKLIN'S GROUSE DURING THE BREEDING SEASON.

INTRODUCTION

Territorial behaviour is presumably important in determining the dispersion and, locally at least, the density of a population of displaying male grouse (Watson 1967; Zwickel and Bendell 1972; Rippin and Boag 1974). A similar relationship between territorial behaviour, dispersion, and density has been suggested for female Franklin's Grouse, Canachites canadensis franklinii, (Herzog and Boag 1977; 1978) and the closely related (Short 1967) female Blue Grouse, Dendragapus obscurus, (Stirling 1968; Zwickel 1972; Hannon 1978).

Herzog and Boag (1978) established that female Franklin's Grouse occupy relatively exclusive areas in spring. These females responded most frequently to tape-recorded playbacks of a female vocalization that MacDonald (1968) called the "aggressive call", during the mating and laying periods (Herzog and Boag 1977). Herzog and Boag (1977) heard females "calling" in apparent response to the tape-recording, but rarely spontaneously, and then only when interacting females were in visual contact. Alway and Boag (1979) reported that captive females used this "call" in aggressive interactions around mating and laying, and sometimes apparently spontaneously, after sunset. However, the behavioural "normality" of these interactions and "calls" could not be assessed because of the unnaturally

high densities at which these captive birds were kept.

Keppie (1975) and Herzog and Boag (1978) noted that some yearling females made extensive movements in spring. Alway and Boag (1979), extrapolating from their observations of captive birds, suggested that such movements were prompted by aggressive interactions in which subordinate yearlings were forced to move into new habitat. Acceptance of this hypothesis requires observational confirmation in the wild.

The means by which breeding females signal territorial ownership to others of their sex in the dense forest (5640 trees/ha - McCourt 1969) that they inhabit is unknown. Do residents repel territorial trespassers through direct physical encounters? If so, how are intruders found on home ranges that vary in size from 0.6 to 37.9 ha (Herzog 1977)? Or are intruders repelled by sounds produced by the residents that signal possession of a territory? Or are combinations of signals and interactions used to secure exclusive use of space? This study attempted to answer these questions.

STUDY AREA

This study was conducted on a 555 ha plot in the eastern foothills (elevation 1500-2000m) of the Rocky Mountains, near the R.B. Miller Biological Station (50° 39', 114° 39' W), 27 km west of Turner Valley, Alberta.

Observations were concentrated on two sub-sections (199 ha), but censusing and additional data were collected from other parts of the area when possible.

Forest cover on the area is dominated by fire-induced lodgepole pine (Pinus contorta). Subdominant tree growth included primarily white spruce (Picea glauca), and isolated clones of aspen (Populus spp.). McCourt (1969) and McLachlin (1970) provide a more detailed description of the habitat used by Franklin's Grouse on this area.

METHODS

The study area was searched for grouse at irregular intervals (3 times/week to 1 time/3 weeks) from 28 April, 1976 to 15 December, 1977. In 1977, this censusing was accomplished more thoroughly with a trained pointer. Censusing was most intensive during and for a two month period prior to observations (see below). All Franklin's Grouse encountered were noted. If unmarked, they were captured with a noosing pole (Zwickel and Bendell 1967) and banded with an individual set of coloured leg bands. Resident birds were recognized on the basis of repeated sightings and records from past years (Keppie 1975; Herzog 1977).

Some residents were radio-tagged in 1977, as early as March, with transmitter packages weighing less than five percent of body weight, and similar in design to those used

by Herzog (1978). Radio-marking has been shown to have minimal effect on the survival and behaviour of grouse (Boag 1972; Boag et al. 1973; Lance and Watson 1977; Herzog 1978). Birds were released at the point of capture and repeatedly located at will with a hand-held yagi antenna. If a radio-tagged bird had to be recaptured to change the transmitter battery after observations commenced, it was slowly herded across a series of noose carpets (Anderson and Hamerstrom 1967). This method of recapture was used when possible, as it seemed to produce less trauma and risk of injury, than the noosing pole which was used only when an individual remained in a tree.

Detailed records of behaviour were obtained by direct continuous field observation over extended periods of time from 28 April to 30 June,1976 and 1 April to 30 June,1977. Individual observation periods ranged from 30 min to 16 hrs but averaged 3 to 4 hrs, 2 to 3 times daily. Individuals that were not radio-tagged were observed opportunistically.

Birds were approached with as little disturbance as possible and then followed unobtrusively from a reasonable viewing distance (5-15 m). No attempt was made to remain concealed. Birds appeared to quickly habituate to the observer, who in most cases, apparently became a readily recognized but non-threatening, non-interacting object in the subject's environment (Goodall 1963; Schaller 1963; Geist 1970). Two radio-tagged individuals did not habituate to the observer's presence, presumably because of trauma

experienced in capture and handling. These birds were excluded from further observation. That most individuals apparently habituated was evidenced by their frequent approach to within a metre of an observer.

All behaviour was recorded as it occurred, on cassette tapes in a hand-held recorder. Additionally, a 200mm f/3.5 (approximately 4-power) telephoto lens on a 35mm SLR camera was used occasionally to view and document movements, postures, and feather positioning.

Rate of ground movement was calculated at irregular intervals (2 to 10 min, depending on activity) from paced measurements, to the nearest metre, along the route of a bird's travel. Derived distances were thus minimal, because measurements did not include all deviations from a straight line made by a wandering bird. Flight distances were measured similarly, but standardized to include only actual ground distance covered, not height. Direction of travel was also noted, initially with a compass, and later in relation to familiarity with known landmarks. Locations of grouse were given coordinates from a grid superimposed on an enlarged aerial photograph of the study area.

Trees frequently used for roosting and other activities were marked with a small ribbon to approximately delineate the boundaries of "territories" (Brown and Orians 1970) and primary activity sites. Boundaries of "home ranges" (op.cit.) were calculated in the same manner as Herzog and Boag (1978). Because of the low frequency of intrasexual

interactions, "territory" has been further defined as the area of observed concentrated (>75%) daily and seasonal movements.

When possible, birds were followed to their roosting sites. Once a bird became inactive for about 20 min following dusk the tree was marked, and the site left as quietly as possible. The following morning, the same site was revisited before dawn to ensure recording when the same bird became active.

The perching height of a bird was measured when possible, but was usually estimated to the nearest 0.5 m, to avoid disturbance.

Tape-recorded field data were transcribed as soon as possible for greatest recollection and accuracy. The duration of a continuous behaviour pattern, for example feeding, was classified to the nearest 15 sec. Non-social behaviour, occurring during a bout of social behaviour, had to occur continuously for more than 5 min before it was recorded as a separate activity, in order to include displacement activities (based on unpublished observational data). For example, a bird interacting with another may have occasionally fed or preened momentarily, but the total time has been recorded as interacting. Time involved in each behavioural category was expressed as a percentage of all observation time of each daylight hour during which observations were conducted. All such hourly frequencies presented are based on total seasonal duration of

observation unless otherwise noted. Different sample sizes have often been presented for different aspects of a single activity, since all aspects could not be keenly scrutinized during all observations.

Biological seasons (periods) were standardized to relate to the behavioural and physiological state of the individual, not to average population parameters.

Data were analyzed using computer packaged Kruskal-Wallis tests unless otherwise specified. When these tests showed significance, post-hoc multiple confidence interval procedures for the Kruskal-Wallis tests were used (Marascuilo and McSweeney 1977). In the calculation of these confidence intervals the 99% level was used.

Representative vocal and non-vocal grouse sounds were recorded with a Uher 4000 Report-L Recorder at 9.5 or 17 cm/s from birds in the wild. These sounds were analysed with a Kay model 6061-B Sona-Graph over a frequency range of 80-8000 Hz. Sonagrams of flight sounds were made using the narrow-band filter, while the wide-band filter was used for vocalizations.

RESULTS

Results of this study are based on more than 500 daylight hours of field observation of 10 individual female grouse (Table 1); most of the data (>75%) were recorded from three radio-tagged hens.

The early spring season of Herzog and Boag (1978) was subdivided into two periods on the basis of observed changes in female behaviour. An "early pre-laying period" was recognized, encompassing the time between establishment of a spring territory and approximately a week before mating. Mating was observed once in the field. Using the known interval between mating and laying of the first egg for this bird (4 days), mating dates for other hens were extrapolated from known laying dates. Alway (1977) also reported a 4-day interval between mating and laying for a captive female. The second period, "late pre-laying", encompassed the interval between the end of the early period and the onset of laying. This is the period when the ovaries of periodic breeders, such as grouse, are in the rapid phase of recrudescence (Hannon 1978), and when resident female Franklin's Grouse were first recorded advertizing (see below).

During early pre-laying females were infrequently seen interacting with other females (Table 1). Three such encounters involved a resident female on an established territory interacting with an intruding yearling female. During these interactions, the resident female always uttered the "call" noted by MacDonald (1968; see above). The same apparent sound was also uttered on occasion by the intruding yearling, but much less frequently. During these encounters, the resident female was never observed chasing or attacking the intruder. Such intruders occasionally remained on the territory throughout an observation period,

but were never sighted on the territory again and usually never encountered on the study area again, in spite of censusing conducted for more than 6 months beyond the observation periods. All such agonistic encounters were recorded only on the territory of a resident (Level 1 - Table 1). Alway and Boag (1979) also noted that interactions among captive females during this period were comparatively passive with respect to action.

During the late pre-laying period, no interactions were observed between any females (Table 1), although yearlings were often encountered in adjacent habitat where they were assumed to be establishing territories in the absence of residents.

It was during this late pre-laying period that a unique female behaviour was first observed. Lone resident females were observed to "spontaneously" utter the same "call" that MacDonald (1968) had recorded in the field during a staged encounter between an adult female and a female dummy. When played back in the field, this sound has been effective in attracting males during the breeding season (McLachlin 1970). The same recording was used by Herzog and Boag (1977) to test seasonal changes in responsiveness of females in the wild to this sound. Much conjecture has arisen about its function(s).

This "call" involves a series of harsh, rapidly repeated (100-120 msec intervals) guttural notes of slightly rising fundamental frequency, which are frequency modulated

at a rate of approximately 30 Hz in a sinusoidal manner. These notes are often followed by a series of whining notes, consisting of an ascending and descending fundamental frequency (Fig. 1). As this "aggressive call" has more than four notes of more than one type which are uttered in succession in a recognizable sequence in time, it is therefore not a "call" but a "cantus" - a form of song that is less rigidly structured than a "canto" (Hjorth 1970). It cannot be considered a "canto", because the combinations of successive notes were not habitually of the same length (see below). Hereafter it will be referred to as the "Cantus" (plural Cantus).

On eleven different occasions females were heard uttering the Cantus in the absence of any apparent stimulus. These "spontaneous" bouts of singing when uttered in the evening, usually occurred some hours after an observation had begun and therefore were apparently not in response to the presence of the observer. The mean duration of a bout of singing was 5.48 min. There was considerable intra- and inter-individual variation in the number of notes uttered by females on different occasions. Each Cantus involved up to eight notes. Each bout of singing recorded in the field consisted of Cantus comprised of primarily the initial staccato-like notes. On two of these "spontaneous" singing occasions, the whining notes of the Cantus followed the staccato notes. The number of Cantus per bout of "spontaneous" singing varied from one to 27, with a mean

rate of 1.6 cantus per min.

Cantus were sung apparently "spontaneously" almost exclusively at dusk and dawn (Table 1), during periods when feeding was usually intense. These Cantus were given irregularly and did not occur every morning and evening after the first noted occurrence from a particular hen. "Spontaneous" Cantus were heard only during late pre-laying and laying (Table 1).

All such singing was given from trees. The majority of Cantus were uttered from lodgepole pine (79%); white spruce (21%) and trembling aspen, Populus tremuloides, (<1%) were also used. The mean height from which Cantus were given was 6.3 m. As females often hopped from tree to tree while feeding and singing, percent and height are based on duration of the total observed singing.

The Cantus was the only female vocalization heard in this study that had an audible range of more than 10 m to the human ear. The Cantus could be heard more than 50 m under ideal conditions.

The "spontaneously" sung Cantus almost always coincided with a high frequency of flights by territorial females at dusk and dawn (Table 1). These flights occurred between trees when feeding was intense, either just before the grouse went to roost at dusk, or immediately after leaving the roost at dawn. They seemed to be more regular than was the singing. However, because of the dense habitat and the distance covered by some of these flights (up to 195 m), it

is probable that some Cantus were not recorded. After a long flight, it often took several minutes to relocate a female, and since hens were usually heard singing within the first few minutes of alighting at a new site, the reported frequency of Cantus occurrence was probably minimal.

All breeding females observed during the late pre-laying and laying periods undertook these twilight flights which tended to zig-zag across the territory, often from one end to the other (Fig. 2). Following each flight, feeding and sometimes singing resumed. Female flight sounds were composed of wing-beat pulses approximately 80 msec apart (Fig. 1).

Overall hourly movements by females were greater ($H=146.54$; $d.f.=3$; $P<0.001$) during the late pre-laying and laying periods than during the early pre-laying, incubating, and post nest-loss stages (Table 1). In addition, the frequency of flights by females was greater ($H=164.27$; $d.f.=3$; $P<0.001$) during the late pre-laying and laying periods than during the other stages. However, flight distances during daylight by late pre-laying and laying females were shorter ($H=26.56$; $d.f.=3$; $P<0.001$) than by females at any other time of the day or study period (Table 1).

One female was observed frequently enough that great familiarity with the topographic and vegetative features on its territory was acquired. For this bird, 63 percent of 56.25 min spent "spontaneously" singing the Cantus took

place from three regularly visited pines. The remaining Cantus were given either from roost trees or at a site where a twilight flight ended. The seasonal change in use of four specific pines on this female's territory is shown in Table 2. A greater proportion (X^2=415.2; d.f.=1; P<0.001) of time was spent by this female in these pines during late pre-laying (64%) and laying (88%), than during early pre-laying (25%) and post-nest loss (20%). These pines were distributed throughout the female's territory (Fig. 3). Typical movements by this female in an evening and the following morning during late pre-laying are shown in Figure 2. Furthermore, this female regularly used at least one of these pines during both years of the study, although data in Table 2 are from the second year of the study only. No females were heard to utter Cantus within 100 m of a prospective nest site.

All observed interactions between females during the laying period were of a more intensely aggressive nature (Level 2 - Table 1) than earlier in the season. They involved only resident territorial females that were presumably laying or newly incubating. Four such interactions involving five different females were observed during the laying periods of two regularly observed females. All involved a high rate of singing the Cantus by both birds. These Cantus always included the initial staccato notes and many of the whining notes. Variation of Cantus, particularly in pitch, could be used to identify individual

females that continued interacting beyond dusk. All such encounters took place with both birds in a tree, never on the ground, as was often the case with interacting males (Nugent 1979). Brief physical contact (buffeting) was observed, but Cantus and flying towards the opponent constituted the majority of agonistic behaviour. The "horizontal aggressive posture", noted by Alway (1977) in aggressively interacting captive females, was never observed in the wild. The adoption of this posture is possibly used by birds in close proximity on the ground.

Unlike observations during early pre-laying, female agonistic interactions during laying occurred primarily around territorial borders, or even completely off the territory. These interactions originated between birds while they fed at dawn or dusk. In most cases, the sound of a flight stimulated movement towards and interaction with a neighboring resident. In one instance, a seemingly spontaneous movement for a considerable distance off territory (700+ m), was necessary for the resident to interact with its neighbour.

By contrast, late incubating females appeared to ignore each other, even when feeding within visual contact. Similarly, females which lost their nests seemed to exhibit much greater social tolerance to the presence of another. Only one note of a Cantus was heard and no further threatening behaviour was shown in female interactions at this time of year (Table 1). The seasonal frequency for this

period (Table 1) may not be representative, since it involved simultaneous observation of only two females throughout one evening.

The area used during late pre-laying by the female which was intensively observed, enclosed more than twice the area used by this female during early pre-laying and following nest loss (Fig. 3).

DISCUSSION

Observations of the behaviour of female Franklin's Grouse in the wild appear to corroborate the suggestion of MacDonald (1968) and Herzog and Boag (1977) that females are territorial and that the Cantus is associated with territoriality. The four encounters observed between females that included attacking and chasing an intruder, indicate that the territories of female Franklin's Grouse are indeed defended areas in the classic sense (Brown 1969), at least during the breeding interval. Defense of territories involved relatively non-stereotyped threat behaviour, primarily the use of the Cantus, and occasionally buffeting flights.

Territorial females approached the site where another female flight sound was heard, stimulating most (75%) of the female aggressive interactions observed in this study. This response suggests that wing-produced sounds, through flight, are apparently used by territorial female Franklin's Grouse

as cues communicating the location of conspecifics to each other. The fact that flights by territorial females were of greater frequency during the twilight hours of the periods when the territory was vigorously defended through aggressive interactions supports this hypothesis even though the proximate stimulus for these flights may be correlated with other factors.

The Cantus and twilight flights are believed to be used as acoustic signals by territorial females. "Advertizing", as opposed to "threat", includes all behaviour having significance as communication between distant conspecifics (Hjorth 1970). Therefore, these acoustic signals are believed to be a form of advertizing that communicates occupancy of space and delineation of a breeding territory by a female to conspecifics in the surrounding habitat. Because the initial staccato notes of the Cantus were most frequent during spontaneous singing, they seem to be concerned primarily with advertizing occupancy of space, while the whining notes that were more prevalent during female agonistic interactions seem to convey the greater aggressive intent. The Cantus may be homologous to the female Blue Grouse "quaver cry" (Stirling and Bendell 1970), or "cackle" (Hannon 1978), and the whining notes used by female Sage Grouse, Centrocercus urophasianus, during aggressive interactions with other females (Lumsden 1968).

The Cantus would seem to be energetically adaptive for advertizing territoriality by gravid females. Vocal signals

are physiologically economical to produce, travel rapidly, and decay quickly (Hooker 1968). Sounds that carry through forest habitats, as opposed to grass or edge, are characterized by a narrow range of frequencies (1585-2500 Hz) that have a lower sound attenuation than lower or higher frequencies (Morton 1975). Much of the sonic energy of both the initial and whining notes of the Cantus is within this range (Fig. 1). The initial staccato notes however, have a fundamental frequency between 200 Hz and 700 Hz (Fig. 1). The low frequency notes attenuate less than do the higher frequencies, and the wave length is long enough that obstacles cause little muffling (Hjorth 1976). This would be important for communicating in the dense forests inhabited by Franklin's Grouse.

For maximal range of detection, animals should favor positions in their habitat and atmospheric conditions that optimize communication (Wiley and Richards 1978). Low frequencies (200-400 Hz) are deflected maximally by grass (Wahlstrom cited by Hjorth 1976). The floor of much of the pine forest used by these grouse supports a growth of grasses (McCourt 1969; pers.obser.). Advertizing from elevated perches during twilight may have evolved among female Franklin's Grouse as a consequence. Advertizing perches averaged 6.3 m while perching height for other daylight activities was between 3 and 5 m (Nugent unpubl. data). In addition, Hjorth (1976:156) has suggested that "tree-top singing (reduction of deflection due to soft

surface)", and selection of times of the day when very few other avian species perform, may partially compensate for the poor carrying power of a sound.

The advertizing signals used by female Franklin's Grouse are characterized by qualities that tend to make them easy to locate. Marler and Hamilton (cited by Hjorth 1976) state that sounds having abrupt discontinuities, wide frequency range and repetition are easiest to localize. Both the vocal and non-vocal acoustics used by female Franklin's Grouse in territorial advertizing possess these properties (Fig. 1).

The above characteristics of advertizing sounds presumably enable them to be perceptible to other grouse at a range likely comparable to that of an average territory, particularly when their flights zig-zag across a territory in the manner noted in this study. The regular use of advertizing perches distributed throughout the territory (Fig. 2) additionally increases the probability that territorial signals reach surrounding conspecifics.

That males are attracted by the Cantus (McLachlin 1970) was thought to indicate that at least two females were in the vicinity and interacting. Observations during this study indicate that this is often not the case. Males are probably attracted to singing females because peak advertizing by females coincides with the peak time of mating. Vocal advertizing by females may thus also inform surrounding males of the physiological state of a female. The observed

increase in rate of display behaviour shown by males in the vicinity of the sounds of an advertizing female (MacDonald 1968; McLachlin 1970; Nugent unpubl. data) suggests that the Cantus may serve to stimulate and synchronize sexual behaviour, as has been similarly suggested for vocalizations of female Black Grouse, Lyrurus tetrix, (Koivisto 1965), and Blue Grouse (Stirling and Bendell 1970). Songs in avian females are presumed to promote the mating bond (Pettingill 1970) and female calls notifying males of sexual receptivity have been found in many passerines (Armstrong 1963).

Observations from this study therefore support the hypothesis of Alway and Boag (1979) that female aggressive interactions in the early spring, though seemingly mild, appear to be sufficient to evict subordinate yearling females from the area, with some permanence. Data from this study also support Alway's (1977) conclusion that aggressive behaviour of female Franklin's Grouse peaks during pre-laying and laying and subsides rapidly with the onset of incubation. The greater apparent social tolerance and lack of advertizing behaviour by females after nest loss therefore seem to indicate a marked reduction of territoriality. It can of course also be argued that the drop in territorial behaviour reflects a decreased need for advertizement and defense because neighbours are conditioned to the locations of one another. However, Herzog and Boag (1978) concluded that spatially fixed areas were no longer defended after hatching based on the high degree of overlap

in home ranges of resident brood and broodless females during this period. In addition, a corresponding seasonal decrease in aggressive behaviour has been reported for Blue Grouse (Stirling and Bendell 1970; Hannon 1978).

The lack of sightings of non-resident females on the territories of breeding residents during the late pre-laying and laying periods, and the aggressive nature noted among breeding females in this study support the consensus of Alway and Boag (1979) that the aggressive behaviour of resident breeding females may prevent other females from settling on occupied areas, and may be the proximal cause of the dispersal noted among yearlings (Herzog and Boag 1978). Significantly, these were the only two periods, during more than 700 hours of observation in the field, when territorial advertizing, by females "spontaneously" singing the Cantus, and an increased rate of twilight flights occurred. The observed inclination of non-resident non-territorial females to depart from areas occupied by established females, indicates the extent to which social intolerance may operate to realize a dispersed pattern of distribution among territorial birds.

The observed pattern of comparatively greater daily movements of resident adult females during late pre-laying and laying (Table 1) was similar to that recorded by Herzog and Boag (1978) in late spring. The suggestion by Herzog and Boag (1978) that these movements may indicate patrolling of small areas by territorial females is supported by

observations in this study of attentive and advertizing behaviour associated with greater hourly overall movements and flight rates by late pre-laying and laying females.

The observed difference in the size of the area used by a female when it was most territorial (late pre-laying and laying), and when it was less so, for example the post nest-loss period (Fig. 3), indicated that females were occupying an area that encompassed more resources than seemed necessary to survive, particularly when they can live on a much smaller area during other parts of the year (Herzog and Boag 1978). Maxson (1978) also found that the mean home ranges of female Ruffed Grouse were greatest during pre-laying. If food resource requirements were limiting, one might expect females to be involved in feeding the majority of the time. The greatest mean daily frequency for feeding was by laying females (35 % - Nugent unpubl. data); even during this important energetic period these females rested during the majority of the day (52 % - Nugent unpubl. data). Territories therefore appear to encompass more than enough nutrient resources for females through all seasons studied.

Defense of a territory enlarged beyond that providing just enough resources, follows Verner's (1977) "super-territory hypothesis". The adaptive value of this type of territoriality is linked with an individual's chances of increasing its relative contribution to the gene pool by reducing the absolute number contributed by

conspecifics. Through interactions among themselves, resident females appear to limit access of other females to the resources of an area, including potential mates. No yearling females were ever seen interacting with males throughout the 700+ hours of field observation, despite the fact that male display behaviour towards females comprised 23 percent of all observed male activity in spring (Nugent in prep.). Herzog and Boag (1978) also found that although some yearling females made extensive movements in early spring, they did not remain long in one locality and by late spring occupied virtually exclusive areas peripheral to males. Only resident female territories significantly overlapped male territories.

Evidence thus indicates that the ability of a female to dominate others of its sex in a population of Franklin's Grouse, may be important in maintaining "super-territories" to optimize gene pool input. Further research in this direction is suggested. By preventing other females from obtaining a territory and breeding, or forcing them into suboptimal habitat where breeding success may be lower, an individual female Franklin's Grouse may reduce competition for itself and its offspring for potentially limiting resources during critical seasons. Thus, an individual's offspring could comprise a larger proportion of the total cohort of young produced by the breeding population.

To this end, female Franklin's Grouse appear to have evolved a means of establishing and defending their

respective territories by acoustically signalling occupation of a space, vocally and non-vocally, and by expelling territorial intruders of the same sex through aggressive interaction. Such a situation may also exist among the similarly solitary territorial female Blue Grouse (Hannon 1978).

Table 1. Hourly and seasonal movements and frequencies of social behaviour among female Franklin's Grouse: a. early pre-laying period(n=3335 min.obser.); b. late pre-laying period(n=8370 min.obser.); c. laying period(n=7276 min.obser.); d. incubating period(n=9398 min.obser.); e. post nest loss period (n=2808.5 min.obser.).

Time Interval (MST)	Period	Minutes Of Observation	Mean Hourly Flight Movement (m)	Mean Hourly Number Flights	Mean Total Hourly Movement (m)	Aggressive Interaction among Females (hourly %)** Level 1	Level 2	Spontaneous Advertizing with Cantus (hourly %)**
DAWN (0300-0500)	a	45*	19.4	1.4	36.7	0	0	0
	b	435	131.0	2.2	184.8	0	0	9.88
	c	966	73.9	2.1	112.1	0	2.70	1.20
	d	580	1.3	0.2	3.6	0	0	0
	e	270	3.1	0.4	4.3	0	0	0
DAY (0500-2000)	a	3135	1.3	0.5	42.7	2.35	0	0
	b	6684	2.7	0.5	37.9	0	0	0.50
	c	5300	0.4	0.5	53.5	0	0	0
	d	7933	5.9	0.2	7.4	0	0	0
	e	2115	2.8	0.3	31.3	3.73	0	0
DUSK (2000-2200)	a	115*	12.1	0.4	21.5	13.03	0	0
	b	1240	41.6	2.1	73.5	0	0	9.50
	c	1010	46.9	2.6	105.4	0	3.57	0.02
	d	885	40.7	0.8	43.5	0	0	0
	e	423.5	18.8	1.9	32.5	45.99	0	0

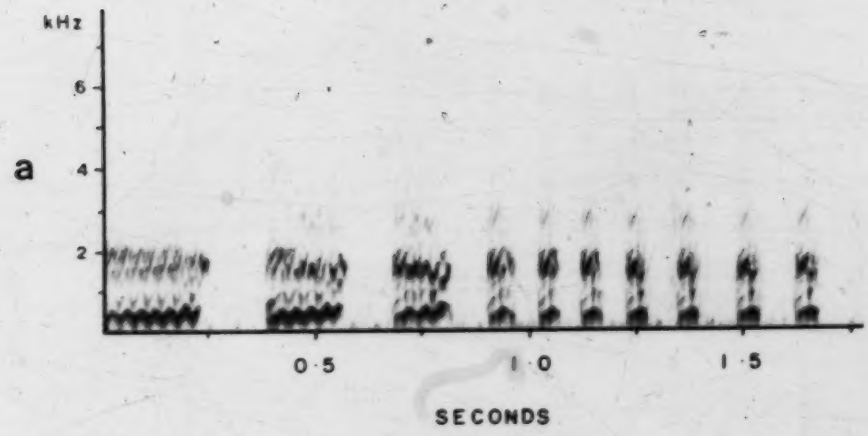
*small observation sample because of high roosting frequency.
**hourly % was calculated from the total observation time during the designated time interval of each period.

Table 2. Time spent in pines by a female Franklin's Grouse.

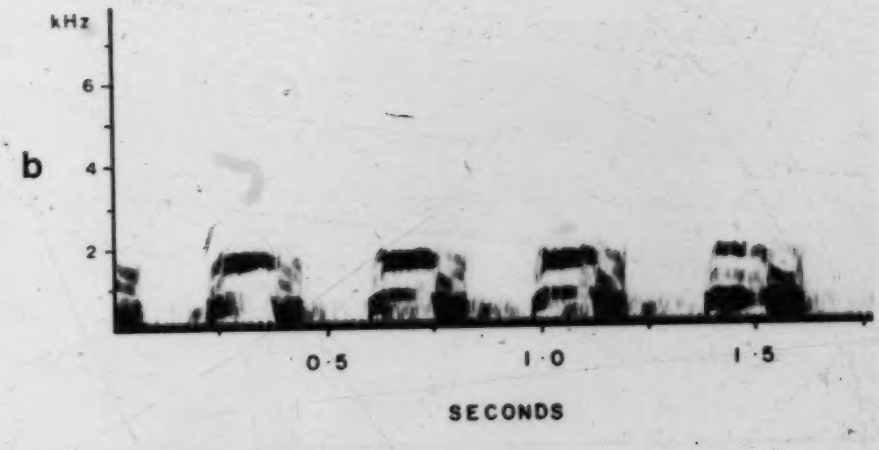
Period	Four Marked Pines		All Other Pines	
	min obser.	(%)	min obser.	(%)
early pre-laying	60	(25.1)	179	(74.9)
late pre-laying	1075.50	(64.2)	600.25	(35.8)
laying	269.75	(87.5)	38.50	(12.5)
incubation	0	(0)	0	(0)
post nest loss	82	(20.1)	325	(79.9)

Figure 1. Sonograms of vocal and wing-produced sounds of female Franklin's Grouse: a. initial notes of Cantus; b. whining notes of Cantus; c. flight.

TYPE S/60 SONAGRAM © KAY ELEMETRICS CO. PINE BROOK, N. J.



TYPE S 60 SONAGRAM © KAY ELECTRIC CO. PINE BROOK, N. J.



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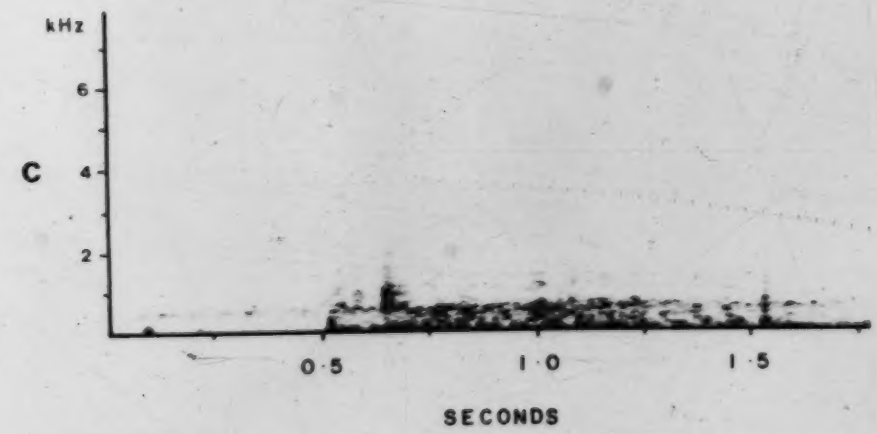

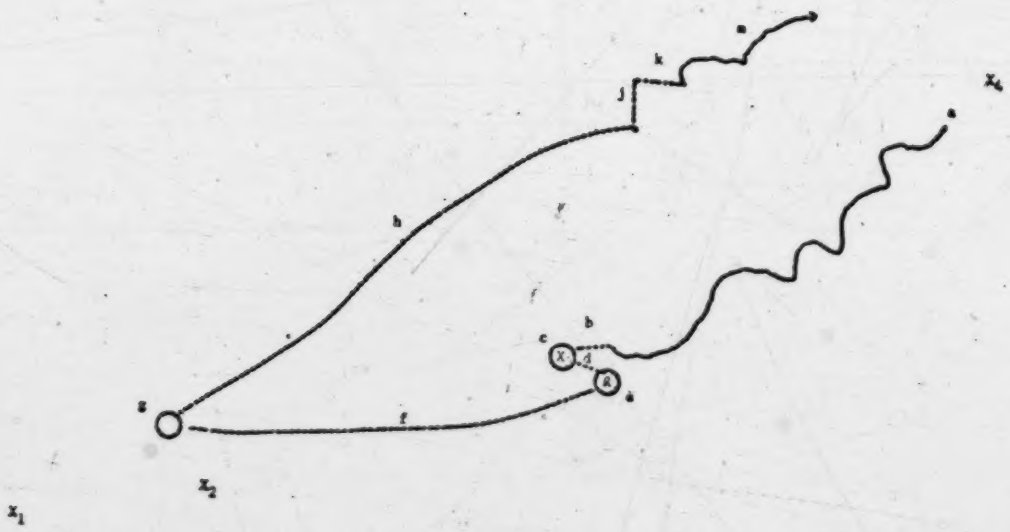

Figure 2. Typical movements by a female Franklin's Grouse from evening to the following morning during the late pre-laying period. Cantus were uttered at circled sites: a. foraging (2000+); b. fly up(2129); c. advertize(2135-2147); d. fly to roost(2156); e. advertize(0452-0504); f. fly 125m(0504); g. advertize(?-0506); h. fly 195m(0520) and advertize(?); j. fly 10m(0532); k. fly to ground (0543); m. foraging(0543+). Scale : 1cm=25m.

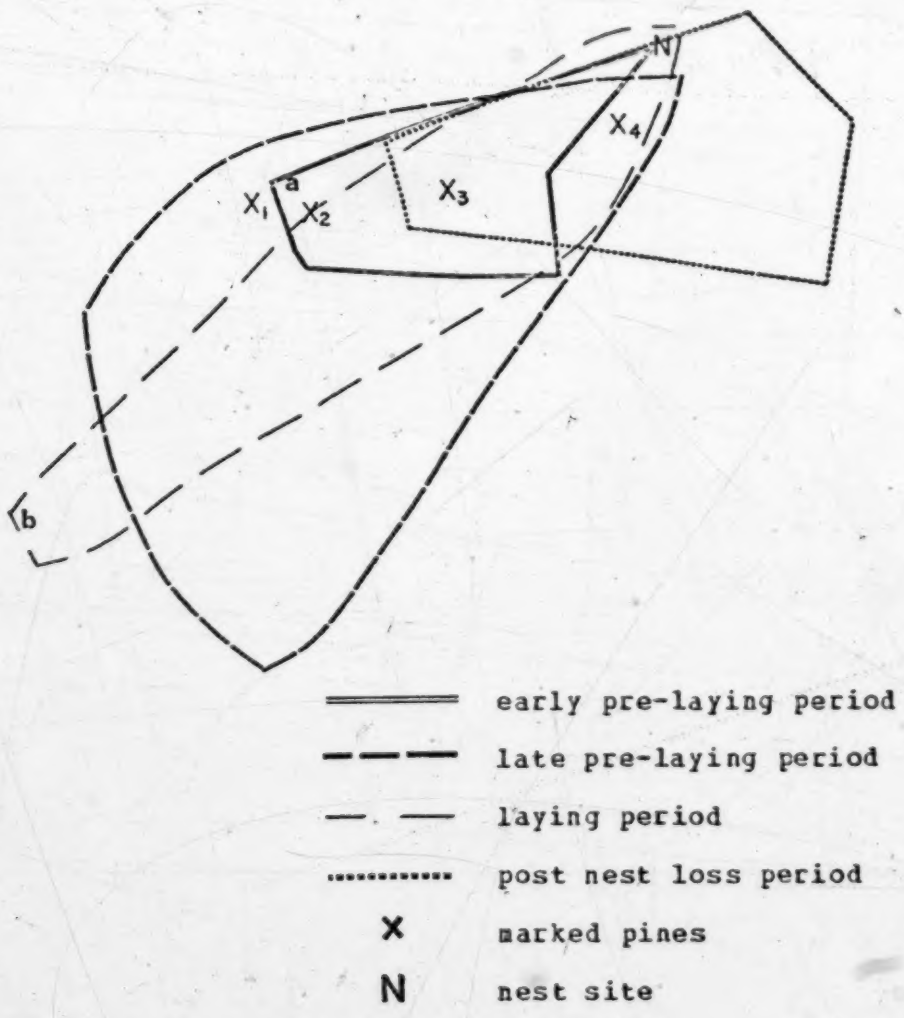

Figure 3. Seasonal home range boundaries of a female Franklin's Grouse (same female as in Figure 2). Movements in all seasons were concentrated in the area between X1 and X4 (ie. territory): a. interaction with an intruding yearling; b. interaction with an adjacent resident female. Scale : 1cm=80m .

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PAPER 2. A QUANTITATIVE ANALYSIS OF ADVERTIZING AND INTRASEXUAL THREAT BEHAVIOUR BY TERRITORIAL MALE FRANKLIN'S GROUSE

INTRODUCTION

Adult and some yearling males of Franklin's race of Spruce Grouse, Canachites canadensis franklinii, occupy relatively exclusive territories in spring (MacDonald 1968; Herzog and Boag 1978). Some of these territories tend to be clumped (McLachlin 1970; Herzog and Boag 1978). However, the means by which this spacing is accomplished is poorly understood. Each territorial male requires a means of influencing other males, as well as females, often over considerable distances, in addition to a system of communication by which it can convey its status and motivation to territory intruders at close range (Hjorth 1970).

Although many displays of males of this species have been described (Lumsden 1961; MacDonald 1968; Hjorth 1970), little is known of their possible function(s) in territorial maintenance and defense. Descriptive accounts of male displays have been based primarily on behaviour under highly artificial situations involving inducement with dummies, mirrors, and playbacks of recorded vocalizations (Lumsden 1961; MacDonald 1968; Harju 1969; Hjorth 1970; Anderson 1973). Because of the difficulty in observing these grouse for prolonged periods in the wild, there have been no quantitative investigations on the seasonal frequency of male displays or their effects on conspecifics. Male

Franklin's Grouse produce a variety of vocalizations and acoustic aerial displays, most notably the Flutter Flight and the diagnostic Flutter Flight cum Wing-claps (MacDonald 1968; Hjorth 1970). However, their respective functions are the subject of speculation. No quantitative investigations exist on the importance of wing-produced sounds for communicating in any tetraonids except Ruffed Grouse, Bonasa umbellus (Aubin 1970; Hjorth 1970; Archibald 1976).

Alway and Boag (1979) suggested that spring dispersal among juvenile Franklin's Grouse (Keppie 1975; Herzog and Boag 1978) is environmentally determined, requiring the stimulus of aggressive interaction with more dominant birds. As their conclusion was based on observations of captive grouse, this behaviour may have been an artifact of enforced proximity during a period when this species is predominantly solitary (Herzog and Boag 1978).

This investigation was conducted to determine how males maintain their spatial distribution and how this spacing may affect the dispersal of juvenile males in spring.

STUDY AREA, METHODS, AND TERMINOLOGY

The study area and duration, observational methodology, and data analysis were similar to those described by Nugent (1979). Terminology used to describe body movements, and postures, as well as previously described Franklin's Grouse displays, is that standardized by Hjorth (1970) unless

otherwise stated. Naming of previously undescribed displays follows ethological convention (Pettingill 1970:260; Hjorth 1970:193). Sequences of behaviour were analyzed with the probabilistic Markov chain analysis technique (Hazlett and Bossert 1965; Slater 1973). Behaviour sequence flow diagrams derived from matrices of observed transition frequencies, include only those acts which had a probability of occurrence greater than 0.02.

Terminology of displays

The full names of displays and other behavioural acts frequently referred to in the text are listed in Table 1. The authority and an abbreviation of each act that will be used in other tables and figures are also listed. If no authority is listed, the display is previously undescribed and/or the terminology is based on personal observation and will be described below. A shortened version of each name that will be used hereafter in the text has also been included in Table 1.

RESULTS

During this study 17 individual territorial males were observed, of which four were radio-tagged (Table 2). Because the behaviour of the latter males was not distinguishable from that of non-radio-tagged males, the observational results have been combined. Data from the radio-tagged

individuals comprised less than 40 percent of total observation.

Two biological periods based on observed changes in male behaviour were recognized. "Spring" encompassed the interval between establishment on a spring territory and peak territorial behaviour. "Early summer" encompassed the period when the majority of females were incubating (Nugent 1979), and males had apparently ceased showing overt territoriality (i.e. June).

Social behaviour of male Franklin's Grouse involved either displays performed "spontaneously", in the sense that no conspecifics were visible and often not audible, or, interaction with conspecifics. According to Hjorth (1970), "advertizing" involves all behaviour having communicative significance for conspecifics at a distance, while "threat" includes the entire range of displays directed towards birds nearby. Threat has been further clarified as aggressive behaviour involving conflict between attack and escape (Pettingill 1970). The following social behaviours have been described under the general category of observed behaviour and are not necessarily classified as advertizing or threat. Social interactions between males and females, although eliciting many behavioural patterns similar to male-male interactions, were believed to be sufficiently different to warrant separate consideration (Nugent in prep.).

Advertizing

The observed frequencies of behaviour patterns involved in ten completely documented advertizing bouts, including spontaneous initiation to termination, are shown in Figure 1. The most frequent behaviour pattern, the Upright (Table 1; Fig. 1), involved all motivation dependent postures along a continuum between an attentive posture and the "Upright" (Hjorth 1970:244). The second most frequent stationary display, Drums (Table 1: Fig. 1), involved one to four wing strokes like the initial drumming movements of a Ruffed Grouse (MacDonald 1968). Drums occurred primarily during early spring and were not performed by all individuals observed. This display was often given immediately following the sounds of other distant displaying Franklin's Grouse. Some males also appeared to give this display in response to the drumming of Ruffed Grouse.

The Flutter Flight (Table 1) was the most frequent mobile display (Fig. 1) and occurred in both vertical directions. Flutter Flights primarily consisted of sonic energy below 1750 Hz and were characterized by wing-beat pulses approximately 65 msec apart (Fig. 2). Males were recorded using only conifers as perches to and from which Flutter Flights were made. More than 75 percent of the upward Flutter Flights involved rising to a perching height between 2 and 4 m.

Wing-claps (Table 1) were the second most frequent mobile display (Fig 1). Wing-claps produced two sonic energy

pulses which occurred 320-340 msec apart (Fig. 2). Forty measured Wing-clap flights averaged 20.6 m in length. Of hundreds observed, only one Wing-claps display terminated in a tree.

"Wing-beat displays" (Hjorth 1970) thus, constituted the majority of all observed male advertizing behaviour involving movement (Fig. 1). The ratio of Flutter Flights to Wing-claps was 3.9:1 (Fig. 1). During advertizing bouts the former occurred at a rate of one every 2.9 min, while the latter occurred only once every 11.4 min (n=578.5 min). Although MacDonald (1968) stated that Wing-claps were audible at about 300 m, the sounds of these displays occasionally carried more than 750 m in this study, especially for birds performing from higher elevations than the receiver, and during relatively calm conditions. It seems safe to assume that grouse hear at least as well as man. The frequency sensitivity thresholds of birds are optimal between one and four kHz, similar to man, but sensitivity to frequencies both lower and higher may be considerably greater than that of man (Schwartzkopff 1968). The rolling terrain of the foothills inhabited by Franklin's Grouse may thus facilitate transmission of advertizing sounds over a greater range than was previously thought (i.e. from hillside to valley bottom and facing hillsides or vice versa). Other flight sounds produced by male Franklin's Grouse carried less than 100 m.

Tail-swaying (Table 1; Fig.1) encompassed a continuum

of movements between normal walking and "Display Walking cum Tail-swaying" (Hjorth 1970:245). Some individuals tended to sway the tail more than others. It was usually these individuals that occasionally performed Tail-fannings (Table 1). The sounds produced by the feathers in these two displays (MacDonald 1968; Hjorth 1970) could not be heard over distances greater than 5 m.

One of the infrequently observed behaviour patterns shown by an advertizing male (Fig. 1) was a display described by Hjorth (1970:246) as "Bowing cum Tail widening". The bills of birds audibly contacted either vegetation or the ground in the majority of my observations of this behaviour, and forest litter or bark was often picked up and scattered. Lumsden (1961) on the other hand, noted that the bill was kept closed at all times when males of the nominate race exhibited this display. Bishop (in Hjorth 1970), Lumsden (1961), Stoneberg (1967), MacDonald (1968), and Anderson (1973) have described this display as pecking rather than ritualized "Bowing". Therefore, I propose that it be called the Pecking Display.

Aggressive calls (Table 1) were very infrequently heard in observations of advertizing males (Fig. 1). Aggressive calls usually had four to six notes comprised of bursts of wide frequency range pulses at 10 msec intervals with a fundamental frequency of 100 Hz (Fig. 2). Other advertizing (Table 1) involved feeding, drinking, and/or comfort movements, that were probable displacement activities.

No observable differences were evident between advertizing behaviour in spring and early summer.

One male (R/B) was observed frequently enough during 1976 to allow familiarity with the topographical and vegetative features of its territory. This bird regularly used specific trees ("display trees" - Anderson 1973) and patches of forest floor ("ground stages" - op.cit.) from which to advertize within regularly frequented areas ("display sites" - op.cit.) on the territory (Fig. 3). For this male, 82 percent of 91 observed Flutter Flights involved four display trees, and 72 percent of 32 Wing-claps involved landing on four ground stages. Ground stages were small circular open areas, averaging 4 m in diameter, near the bases of display trees, upon which Wing-claps and Flutter Flights terminated, and upon which other displays (Fig. 1) occasionally occurred. All display trees on a display site were lodgepole pines, Pinus contorta, and were on alternate ends of a relatively open area, as noted by McLachlin (1970), between which Wing-claps took place. Male R/B usually flew to or from the same branch - "display perch" (Anderson 1973) - of a display tree while advertizing. It was on these perches that males spent the majority of the time while advertizing, and upon which most of the other behaviour patterns noted in this activity occurred (Fig. 1). These pines were rarely used for feeding and were never recorded being used for roosting. During irregular advertizing off of a display site, white spruce,

Picea glauca, were also occasionally used for Flutter Flights. The ratio of time spent in pine or spruce during advertizing bouts was 7.2: 1 (n=1067.5 min observ.), reflecting a measure of fidelity to pines on display sites when advertizing.

Male R/B had a similar but not as frequently used display site within 100 m (Fig. 3). Another male had four such display sites, which were used successively during a bout of advertizing. Anderson (1973) found a similar organization of display sites for C. c. canace in Minnesota. My observations indicated this pattern of display sites was common to all territorial males. In fact, when male R/B was removed, the new resident of this territory, frequented not only the same display sites, but also regularly used the same display trees and perches for advertizing.

Advertizing was virtually the only activity of a male on a display site. Advertizing males spent most of their time in trees (66 percent of 1067.5 min) of which the most significant portion was spent in pines (88 percent of 703.5 min). While advertizing, males spent 78 percent (Table 3) of the time in stationary attentiveness (Upright - Fig. 1), primarily in trees (Table 3). The high frequency of stationary attentiveness exhibited by advertizing males in these display trees suggests that the latter were important components of the territories of male Franklin's Grouse.

The results of a sequential analysis of the behaviour patterns involved in advertizing are graphically depicted in

Figure 4 (see Appendix 1 for transition frequency matrix). They are best described in relation to the habitat used. Flutter Flights were most frequently preceded and followed by an Upright. That is, a male assuming an Upright on a ground stage frequently flew (Flutter Flight) up to a display perch in a display tree and reassumed an Upright. Subsequently, a male most frequently flew (Flutter Flight) down to the ground stage from which it originated, or it Wing-clapped and alighted on a second ground stage. Following this Wing-claps, a male most frequently adopted the Upright, but often Tail-swayed closer to a display tree, or even momentarily engaged in some maintenance behaviour (Oa). This sequence was often followed by a Flutter Flight up to a display perch in a second display tree, and in addition to assuming an Upright, a male often Drummed, or alternately flew (Flutter Flight) down on to the second ground stage. If it Drummed, there was a tendency to Drum again or to adopt an Upright. Drums seemed to occur as frequently from a perch as on the ground. Drums also followed Flutter Flights or Wing-claps, but less frequently.

In this manner, an advertizing male tended to alternate back and forth between opposing display trees by Wing-claps, or occasionally by Tail-swaying. Tail-fannings in advertizing seemed to proceed mainly from an Upright. Tail-fannings usually occurred while a male was in a display tree (cf. "threat" below), involving rapid lateral movement along a branch.

Advertizing occurred over most of the study period (Table 2). Advertizing was the major behavioural activity of territorial males around sunrise and sunset during spring, but only around evening in early summer (Table 2). The proportion of time spent advertizing during spring was nearly three times greater than in early summer (Table 2 and Table 3). This was primarily because in both years of the study, the majority of advertizing ceased early in the early summer period.

During peak advertizing in spring, this activity occurred frequently in the early morning, and much of the evening, but rarely in between. The small peak of advertizing evident around midday during spring (Table 2) primarily involved yearlings that were presumably establishing on a territory, or a male displaying to a distant female during the period of peak mating. In one such instance, a male was observed to repeatedly switch between threatening and advertizing behaviour while a female was on his territory. This advertizing seemed opportunistic in that it did not take place at a regular display site, but occurred at various locations within the acoustic range of a moving female, which was frequently out of visual range of the advertizing male. In contrast to Archibald's (1976) recording of nocturnal drumming by Ruffed Grouse, sounds of male Franklin's Grouse advertizing, during an observation from early evening to the following morning, at the seasonal peak of advertizing in 1976, were not heard after dusk nor

before dawn in the vicinity of three displaying males.

In 1976 a group of four territorial males were observed advertizing relatively frequently until as late as 14 June. These males were frequently heard to Flutter Flight or Wing-clap in apparent response to the same sound from a neighbour, and seemed to have a greater rate of wing-beat displaying than males located in areas of lower density. However, there was little evidence of any hierarchial order among the members of this "territorial community" (Baerends cited by Kruijt and Hogan 1967).

The mean duration of a bout of advertizing was 57.9 min (Table 3), ranging from 5 to 165 min. The average absolute distance moved during a bout of advertizing was 153.2 m in flight and 40.6 m walking (Table 3). Thus, advertizing males accomplished 72 percent (Table 3) of observed displacement by flight. The mean number of flights (ie. Flutter Flights, Wing-claps, and occasional other flights) for a bout of advertizing was 25.5 (Table 3), ranging from 4 to 102. Overall hourly movements by males in spring were greatest during the early morning, evening, and twilight intervals (Table 2) and were greater ($H=34.34$; $d.f.=5$; $P<0.001$) during the early morning and evening of spring than during the corresponding interval of summer. This difference reflects a decrease in advertizing frequency during this interval (Table 2). Overall hourly movements by males in spring were not significantly different from those of late pre-laying and laying females (the only season when females were

observed advertizing - Nugent 1979), but were greater than those of females at any other time ($H=192.12$; $d.f.=7$; $P<0.001$). In addition, the hourly frequency of flights by males in spring was greater ($H=220.70$; $d.f.=7$; $P<0.001$) than by any other cohort at any other time of the study period.

Threat

With the appearance of an intruder, advertizing behaviour often developed into threat behaviour, which involved displays never observed if a conspecific was not in view. Sixteen threat interactions were observed between a territorial male and another male during more than 178 hours of field observation of males (Table 2).

Two patterns of threat behaviour were evident. The first (Type A - Table 2) involved overt aggressive behaviour. Fourteen such interactions were fully documented. These interactions involved relatively stereotyped behaviour. Typical behaviour patterns shown by a threatening male are shown in Figure 1. Although territorial yearling males were rarely encountered, threat behaviour displayed by such males was included in this analysis, as it did not seem different from that displayed by older males. The most frequent behaviour patterns were the Upright and Tail-swaying, described above in advertizing. A frequently seen, yet previously undescribed pattern, the Upright Advance, included travel in an Upright posture without any tail swaying. As it appeared to be an intermediate form

between normal walking and "Display Walking cum Tail-swaying" (Hjorth 1970), it has been included in the Tail-swaying classification. Pecking Displays and aggressive calls were next highest in frequency, followed by Tail-fannings, Other threat (Table 1), and Flutter Flights. Tail-flicking (Table 1; Fig. 1) involved rapid fanning and shutting of the lateral rectrices and was usually accompanied by aggressive calls. Aggressive calls were repeated most frequently when a resident was in view of an intruder, and more frequently the closer the males. Other threat (Fig. 1) primarily included presumed displacement activities such as temporarily moving away, comfort movements, and feeding.

A Wing-claps display was witnessed only once in threat behaviour (Fig. 1) and was immediately followed by the performer Tail-swaying toward the intruder. Fighting (Fig. 1) was observed briefly (<10 sec) only once and was followed by an older resident male chasing a fleeing intruder in flight. Fighting mainly involved the males buffeting each other with their wings; no pecking of an opponent was detected. Watson and Jenkins (1964) also found that actual fighting usually lasted less than 5 sec in Red Grouse, Lagopus l. scoticus.

Less frequent but diagnostic of male threat behaviour were Driving Flights, Forward Arcing, and the Forward Rush (Table 1; Fig. 1). Forward Arcing included a posture with the neck tipped forward and the tail either tipped upwards

slightly, or held horizontally, but folded or fanned minimally (Fig. 5). In this posture, a male strutted with long steps back and forth in small incomplete circles around and approximately 1 to 2 m from a trespasser. If the intruder was in a tree, the strutting took a different form - Circling (Table 1; Fig. 1) - which occurred in much larger arcs, approximately 5 m from the base of the tree in which the intruder was perched. This form of strutting somewhat resembled "Display Walking cum Tail-swaying" (Hjorth 1970), but with much less exaggerated movements and plumage arrangements. Although the combs were engorged during all threat displays, they seemed to be maximally expanded by the aggressor during Forward Arcing. Occasionally if an intruder had not fled in response to any of the above acts (most did), a male rushed directly at it in a Forward Rush, a posture with a very pronounced forward inclination of the neck and generally horizontal body profile (Fig. 5). Some apparently intensely aroused individuals moved towards or chased intruders over long distances (> 100 m), while displaying the Forward Rush. Intense aggressive calling often accompanied the Forward Rush. As a Forward Rush was often very short in duration, it was difficult to determine whether a male rushing at another with open bill was attempting to vocalize or peck its opponent. The relatively low frequencies (Fig. 1) of Forward Arcing and Forward Rush, displays performed primarily on the ground, reflect the recording of most intruders in trees. A Driving Flight

involved a flight in the direction and subsequently in pursuit of a trespasser, and was effective in chasing an intruder away from the territory.

A sequential analysis of the behaviour patterns frequently observed during threat interactions is illustrated in Figure 6 (see Appendix 2 for transition frequency matrix). An Upright, the initial response to an intruder's flight sound, led to the male Tail-swaying, or sometimes flying (Fig. 1), in the direction of a presumed intruder. This Tail-swaying involved frequent stops in an Upright, with frequent head cocking and turning presumably to search for further clues of the intruder's location. Occasionally while travelling, a male would perform a Tail-fannings in a direction that invariably proved to be where the intruder was located. Males seemed able to sight an intruder in the dense forest (4514 stems/ha - McLachlin 1970:15) more readily than the human observer. More frequently, Tail-fannings were not elicited until the resident was in close proximity to an intruder, and most frequently when the intruder was sighted in a tree. The "Hiss and Squeak" vocalization (Lumsden 1961) that accompanies this display in the nominate race, was never heard during this study, despite the fact that the observer was often less than 2 m from males performing this display. Tail-fannings most frequently preceded an Upright or a Pecking Display. Pecking Displays commonly elicited more Pecking Displays, or led to Tail-swaying or an Upright.

If the intruder was in a tree, and remained, a Pecking Display was commonly followed by Circling, which often led to further Pecking Displays or an Upright (Fig. 6). That is, a resident circling the tree in which an intruder was perched often stopped in an Upright and cocked its head, apparently appraising the intruder, then performed a Pecking Display, and reassumed an Upright. Occasionally, a male then flew (Flutter Flight) up into an adjacent tree and assumed an Upright but soon flew (Flutter Flight) down to repeat any combination of the above. This was often sufficient to cause the intruder to fly from the territory, closely followed by the resident male in a Driving Flight. Some males continued aggressive calling during Driving Flights.

Most interactions culminated with one or more of these Driving Flights (Fig. 6), in which the resident flew after and sometimes continually flushed an intruder, until it was driven from the territory. As most intruders never flew out of hearing distance, some males chased after them on the ground in a Forward Rush and repeatedly displayed portions or all of the above sequences until the intruder had been "escorted" off the presumed territory.

If the intruder was encountered on the ground, any combinations of the sequences possible in Figure 6 occurred, with the exception of Flutter Flights and Circling. Forward Arcing seemed to represent a more intense form of circling which occurred when an intruder was on the ground. Thus, in close proximity to an intruder, vigourous Forward Arcing,

maximal comb expansion, and frequent aggressive calling were displayed. Once this stage of behaviour was exhibited by a territorial male, further threat behaviour sequences were rarely necessary. The intruder either fled (always in flight), or was charged at in a Forward Rush; in either case, the intruder fled and the resident followed with a Driving Flight. Forward Arcing occasionally occurred in the branches of a tree, when an intruder had fled and a resident had followed it in a Driving Flight. Rarely did a resident fail to fly after a retreating intruder.

The interaction involving the only Fight observed was also the only case in which a Forward Rush (immediately followed by the Fight) was not preceded by any other threat behaviour (Fig. 6). This encounter occurred late in the breeding season along a presumed mutual territory boundary between a resident adult and a newly established yearling on a contiguous territory. The latter territory had been unsuccessfully occupied by a succession of temporary yearling territory holders since late winter, but after this Fight, was successfully held.

The latest observed interaction of Type A (Table 2) was on 28 June, although the remainder occurred between 27 April and 2 June.

All but one of these encounters, in which a territorial male had been observed for a substantial period before the encounter, involved the male immediately approaching the site from which the sound of a flight had emanated. The

exception involved the most violent interaction witnessed (Fight) between an older territorial male suddenly moving slowly but directly toward the site of a yearling male established on a contiguous territory. No flight sound was heard during this observation, but because of the wind, it may have been undetected by the observer but not by the adult male. In two instances, although a flight sound was heard, no intruder was seen by the observer. The movement of the resident in the direction of the flight sound may have been sufficient to prevent further trespassing.

Two other instances involved interactions between yearling males attempting to occupy the same territory. The remaining interactions occurred between a territorial male and a yearling male trespassing on the former's territory.

All observed threat interactions involved participants of apparently unequal status, as the trespasser fled the resident aggressor in all cases, and returned none of the threat behaviour exhibited by the territorial owner, except for the one brief Fight observed. Such behaviour may of course be related to peck dominance dependant upon the encounter site location relative to the territory centre (McBride 1971). Most of the retreating yearlings were never observed on the study area again. One of these males however, after surviving the winter in presumed suboptimal peripheral habitat, did occupy a vacant territory from which it had previously been driven (Driving Flight) as a yearling.

In all cases observed, the intruder fled, presumably because all observed interactions occurred on a more dominant resident's territory. The dominant individual was identified by the threatening postures which it assumed. Many times it seemed that an intruder showed very strong escape tendency by the manner in which it looked away from the resident and towards a potential escape route. Otherwise, most trespassers exhibited complete immobility until the final retreat. In fact, in close proximity the behaviour and appearance of an intruder (Fig. 5) were the antithesis of the dominating resident. Although the intruder rarely moved, the resident was almost constantly moving. The resident stood tall with extended neck, while the intruder squatted low to the substrate with a very withdrawn but upright neck, like the typical female tetraonid solicitation posture (Hjorth 1970). Whereas the resident displayed extremely prominent expanded combs, those of the intruder were comparatively inconspicuous. The white "V" marking on the throat of the resident was quite conspicuous, while that of the intruder was much less so. The resident vocalized (aggressive calls) almost continuously, but the intruder appeared to be silent. The tail of the resident was tipped upward and frequently flicked (Tail-flicking - Fig. 1), while that of the intruder was tightly folded and held against the substrate. The feathers of the resident were relatively sleeked, particularily in Forward Arcing and Forward Rush, whereas those of the intruder were more fluffed. This

fluffing exaggerated the white spots along the sides of the submissive bird, contributing to a duller and lighter coloured female-like plumage than that of the resident. By contrast, the side spots of the sleeked plumage of the resident were relatively inconspicuous, giving the body a much blacker appearance.

This type of threat occurred more frequently in spring than in early summer (Table 2). The duration of a threat interaction, from initial detection and response to a flight sound, until the last Driving Flight observed, varied from 2 to 65.5 min with an average of 21.2 min (Table 3). Threatening males were mobile on the ground the majority of the time (Table 3). Most of the stationary postures (Fig. 1) occurred during the initial search for and movement towards an intruder. Males in threat behaviour flew 38.4 m in flight and walked 171.3 m on the average per threat bout (Table 3). Only 35 percent of a threatening male's movement was accomplished by flight. The majority of the walking was involved in search and movement towards an intruder, indicating the average distance from which an intruder could be detected by a territorial resident. The flight displacement represented primarily Driving Flights and was minimal as some interactions involved movement of the interacting birds out of the observer's sight; further flight sounds were sometimes heard, but could not be confirmed. The number of flights observed during a threat interaction ranged from 0 to 6 with an average of 2.1 (Table

3). Thus, threat behaviour involved considerably less flying but greater time spent moving greater distances on the ground than advertizing.

The daily intervals involving the greatest frequency of threat interactions in spring followed the dawn peak and the evening commencement of advertizing (Table 2). This appeared to reflect an attraction of non-territorial yearlings to a site from which advertizing sounds were emanating. Threat was never observed during mid-day when advertizing was least frequent. In early summer the greatest frequency of threat behaviour coincided only with the evening resumption of advertizing (Table 2).

Another comparatively mild form of agonistic behaviour was witnessed in early summer (Type B - Table 2). One interaction of this sort was observed in mid June, about the time that male advertizing ceased. This incident involved two territorial males feeding and resting in a pine along a presumed mutual territory boundary. The behaviour patterns exhibited by these males were comparatively unstructured and thus were not included in the previous analysis. Although the males frequently exchanged aggressive calls, the calls were of such a low intensity that they were often inaudible beyond 5 m. One individual initially gave a few Tail-fannings, yet the pair remained within 1 to 3 m of each other for over 3 hours (and possibly much longer as an evening thunderstorm terminated the observation) with no further signs of the threat behaviour exhibited by these

males earlier in the season.

The long simultaneous observation of these males accounts for the high seasonal frequency (Table 3) of this mild form of threat. Although this frequency may not be representative, this type of male social interaction is believed to be representative, as similiar interactions were occurring amongst females that were not incubating or brooding during this same period (Nugent 1979). Furthermore, males that were observed in close proximity to a female at this time of year displayed no noticeable "threat" behaviour.

DISCUSSION

Advertizing was the only male behaviour observed that frequently occurred in the apparent absence of any external stimulus, and that lacked any apparent maintenance function, such as feeding or preening. Male advertizing was accomplished primarily with the Flutter Flight, Wing-claps, and Drums displays (Table 3). No male vocal signals with any appreciable range (>20 m) were heard throughout the study. The aggressive call is relatively unstructured compared to the corresponding "Cantus" of females (Nugent 1979). Vocalizations therefore, seem to play a minor role in male advertizing.

The hourly flight rates and overall movements by territorial males in spring was significantly greater during

most of the day than any other non-advertizing cohort of the population at any other time of the study period, primarily as a consequence of wing-beat displays in advertizing behaviour. There is obviously a cost connected with advertizing, and the energy so used is unavailable for other purposes (Klopfer and Hatch 1968). It is inconceivable that an activity demanding such a large amount of a bird's time (Table 3) and energy would survive the rigcrs of natural selection unless it had adaptive advantages for the individual.

Flutter Flights and Wing-claps are particularly adaptive for advertizing in the dense pine fcrest inhabited by male Franklin's Grouse, where visual displays would be relatively ineffective. These advertizing signals were much stronger acoustically than any signals belonging to threat behaviour. These displays, particularly the Wing-claps, possess acoustic qualities which make them practical for communication over considerable distances. Since these Wing-beat displays produce sounds that have abrupt discontinuities, a wide frequency range, and are repetitious (Fig. 2), they can be localized relatively easily (Marler and Hamilton cited by Hjorth 1976).

Hjorth (1970) suggested that solitarily performing grouse such as Franklin's, advertized from a central point of a territory to bird's outside it, but not much farther. However, observations of males having multiple display sites on a territory, in addition to the earlier noted enhancement

provided by the rolling terrain, facilitated transmission of advertizing sounds well beyond the territory of the advertizer in many cases.

The occurrence in advertizing of many of the behaviour patterns shown by threatening males (Fig. 1) indicates that there appears to be a threat component to advertizing, and that there is apparently no sudden transition between advertizing and threat behaviour. The lack of any observed trespassing between adjacent territorial males presumably attests to intrasexually repelling characteristics of advertizing sounds. Established territorial residents therefore, appear to space themselves by mutual avoidance of occupied areas delineated by advertizing.

By contrast to established residents, non-territorial yearling males in spring seemed to be attracted to the site of an advertizing male, leading to threat interactions with a resident. No females were encountered in the area by the observer or the observed males throughout such observations. Only yearling males (vs. adult males) were noted near the display sites of residents, and they interacted with resident males only during the periods following the dawn peak and the evening resurgence of advertizing by residents (Table 2). The probability of these yearlings being found on these locations at these times seems high with respect to census sightings on the rest of the study area. Although these yearlings did not appear to display in response to the resident's advertizing, they were located by making a flight

of unknown motivation and immediately displaced by the territory owner. Bendell and Elliott (1967) also found that "silent" yearling male Blue Grouse, Dendragapus obscurus, were attracted by territorial "hooting" males. On the basis of decreased territorial trespassing in early summer (Table 2) and later in the season (Nugent unpubl. data), it seems then, that mutual avoidance of the territory of another, noted among adult residents but not among yearlings, may be a learned or conditioned response. It appears that non-resident birds may locate preferred habitat in this manner, or may assess a resident for the potential of supplanting it from its territory. Similar types of interaction were observed among resident and yearling females (Nugent 1979). Subsequent threat interaction between an intruder and a territory holder appeared to decide dominance and occupancy of a space. Yearling males apparently intruded on resident male territories very rarely in early summer as indicated by the lower frequency of observed threat interactions (Table 2) and the failure to note such trespassing during censusing in summer.

Though females generally avoided displaying males, during the period of peak mating they often moved towards the sound of an advertizing male. Hjorth (1970) states that a male with a female on its territory does not normally perform wing-beat displays. Such was not always the case in this study. Most advertizing males switched to threat behaviour when a female approached. However in one such

encounter a male repeatedly alternated between advertizing behaviour and then reapproaching and threatening a female on his territory. This alternation of behaviour eventually culminated in the only mating witnessed throughout the study, suggesting that wing-beat displays may have a stimulatory effect on females.

Observations from this study thus support the suggestion of others (MacDonald 1968; Harju 1969; McLachlin 1970; Hjorth 1970; Johnsgard 1973) that wing-produced acoustic signals by male Franklin's Grouse function in advertizing occupancy of a space to conspecifics of both sexes. Advertizing by male Franklin's Grouse appears to additionally correspond functionally to song by passerines, as Hjorth (1970) has similarly suggested for drumming by Ruffed Grouse. The best understood functions of bird song are territorial proclamation (acting to repulse males and to attract females for pair formation), species and individual identification, maintainance of the pair-bond, and physiological synchronization of a mating pair (Smith 1968).

Individual recognition was indicated in this study by observations of advertizing males apparently ignoring (not approaching) the regular advertizing sounds of surrounding neighbours, whereas MacDonald (1968) observed that playbacks of a recording of Wing-claps on the territory of a male immediately motivated the owner to move toward and investigate the source of the sound. However, it may be that the location from which a sound comes is at least as

important as the nature of the sound itself. Beer (1970) suggested that if each territorial bird advertized from set specific locations, the sounds of a non-resident would be distinguishable from residents if it occurred at a locality from which advertizing sounds did not customarily come, and may elicit hostility from a bird whose territory has been trespassed. Evidence from this study suggests this may be true of male Franklin's Grouse; only the sounds of non-residents (territorial intruders) were approached by residents, and territorial males usually advertized from regular display sites within the territory. Spacing patterns of Franklin's Grouse may thus have arisen as a result of distance-dependent behaviour of individuals responding to each other as distance-dependent stimuli, as has been observed in other territorial species (McBride 1976).

Although female territorial intruders were often approached from a distance in the same manner (Tail-swaying) as male intruders, territorial males seemed to be able to determine the sex of an intruder from considerable distances. Male display to females never included behaviour patterns exhibited by males towards intruding males even when they seem to be screened from the conspecific by vegetation. Franklin's Grouse may be able to distinguish the sex of an intruder from its flight sounds. Flutter Flight wing-beat pulses occur approximately 65 msec apart (Fig. 2) whereas corresponding pulses in a female's flight occurred at 80 msec intervals (Nugent 1979). At close range this

difference is detectable to the human ear (pers. observ.) and the temporal resolution of sounds by the avian ear is reportedly superior to that of man (Schwartzkopff 1968; Wilkinson and Howse 1975). Information may therefore be encoded in the advertizing sounds of grouse and may be important in individual recognition as well.

To an observer, the advertizing displays of male Franklin's Grouse are conspicuous both acoustically and visually. Male Red-wing Blackbirds, Agelaius phoeniceus, also employ a dual modality communication system (Peek 1972; Smith 1972, 1975). Song and visual displays in this species are presumed to contain similar information (op.cit.). MacDonald (1968) has suggested that the bold black and white markings of male Franklin's Grouse in display, may function as visual communicative signals. The display markings definitely render an otherwise cryptic bird very conspicuous, and my observations of territorial males sighting intruders from considerable distances in the dense forest suggest the visual acuity of these birds is very keen. However, as Hjorth (1970) concluded, it appears indisputable that forest grouse plumage structures or patterns are inefficient in dense wooded terrain as optical advertizing signals toward distant conspecifics. The vigorous movements involved in advertizing in male Franklin's Grouse appear to be more important as optic signals than plumage patterns which tend to be blurred during movements. The advantage of crypticity seems to have

had a stronger influence than the demand for conspicuousness (Marler 1968) in the evolution of plumage signals in advertizing in male Franklin's Grouse. However, as with Red-winged Blackbirds, it is possible that non-acoustic elements are as important in male Franklin's Grouse advertizing, as they are in threat behaviour. The visual and acoustic modalities may act synergistically or additively, but the acoustic modality seems to act as the long distance advertizing signal.

The male mentioned earlier, that used at least four display sites, also had the longest recorded bouts of advertizing and apparently the largest territory. Hjorth (1970) noticed a tendency to more persistent advertizing by lekking species males having larger territories, than by males with restricted space, but felt the opposite was true among solitarily displaying forest grouse. My observations of 5 regularly observed males suggest that Franklin's Grouse advertizing may occupy more time among males with larger territories than small, as in the lekking grouse. This may have a limiting effect on maximum territory size.

Advertizing thus appears to be one of the methods used to establish and maintain a territory by male Franklin's Grouse. Establishment and maintenance of a territory however, appears to also involve relatively frequent defensive action by the owner against trespassers, as witnessed between a succession of yearlings attempting to occupy the same territory. Active defense through threat

interactions were also evident among all older territorial males toward intruding yearling males during the spring dispersal phase of yearlings.

Territorial male Franklin's Grouse actively defended the space they occupied through threat involving both visual and acoustic components, and only infrequently, by actual fighting. Threat seemed to be elicited by the presence of any territory trespasser, male or female. However, threat directed toward females included different display patterns than those used in male-male interactions (eg. "Crouching cum Head-shaking" - Hjorth 1970: 248) and will be discussed elsewhere (Nugent in prep.).

Aggressive calls occurred separately as well as with many threat displays (Fig. 1). The short detection range of aggressive calls appears to make them adaptive to threat, as many male social interactions occurred on the ground where birds are presumably more vulnerable to predators, than in trees.

Forward Arcing and Circling, included a circling or herding manoeuvre. Hamerstrom and Hamerstrom (1960) and Hjorth (1970) suggested this type of behaviour functions to block escape by females from the territory. Observations from this study suggest that these displays function in inducing a male trespasser to retreat, and may also indicate the direction of such, by repeatedly blocking further movement onto the territory. Retreating birds followed this convention in most cases. Forward Arcing and Circling

therefore, appear to be homologous to "circling" (Hjorth 1970) in other grouse, and are very similar to the "threatening approach" described by Watson (1972) for Rock Ptarmigan, Lagopus mutus. The leading edge of the wings were not exposed by male Franklin's Grouse in this display, indicating a strong attack rather than escape tendency (Hjorth 1970).

Hjorth (1970) observed that "Forward displays" were assumed only briefly in forest grouse. The display of a Forward Rush by a male Franklin's Grouse while chasing an intruder over relatively long distances disputes Hjorth's statement, which possibly reflects the paucity of comparative data on male agonistic interactions in any of the forest grouse. The Forward Rush appears to have its homologue in the "fighting" posture noted by Bump et al. (1947) in Ruffed Grouse, the "facing" posture of Red Grouse (Watson and Jenkins 1964) and the "threatening horizontal position" of fighting Rock Ptarmigan (MacDonald 1970).

Hjorth (1970: Fig. 146) presented a functional classification of male grouse threat displays directed towards other males, which ranged from weak to intense. My observations from birds under natural conditions do not support his classification of intense threat by male Franklin's Grouse. The Upright Advance appears to be intermediate in intensity between the "Upright" (Hjorth 1970) and "Display Walking cum Tail-swaying" (Hjorth 1970). The Forward Rush appears to be the most intense threat

display towards males, while Forward Arcing seems only slightly less intense. These interpretations are based on personal observations and Hjorth's (1970) conclusions that a low-breast posture indicates an attack intention, and that the more the head is lowered, the more the display relates to actual pecking of the opponent. Therefore, Tail-fannings which were observed in advertizing, as well as in threat towards males and females, seems to represent less intense threat than was suggested by Hjorth (op.cit). This proposed classification concurs with Hjorth's suggestion that the majority of intensely threatening male grouse adopt a Forward.

The vigorous pecking, detachment and pick-up of vegetation or other substances during a Pecking Display are reminiscent of those in feeding, but the violence of this action suggests a thwarted approach tendency and a strong re-directed aggressive pecking tendency. Pecking Display therefore, replaces "Bowing cum Tail widening", which was rarely observed as described by Hjorth (1970: 246) and most frequently involved vigorous ground pecking, instead of ceremonial "bowing".

Appeasement behaviour of a male towards a more dominant male seemed to involve the adoption of a submissive posture that was female or juvenile-like in resemblance. This posture seemed to be very effective in diverting an opponent's aggression, for no males exhibiting this posture were ever attacked by their opponent. This fluffed, hunched,

spheroid attitude observed in submissive males, was also observed by Hjorth (1970) among lekking males confronting each other along territory borders after displaying. As Hjorth has suggested, this posture appears to be an "inter-individual distance reducing" posture signal (Morris cited by Hjorth 1970). The intense display of combs and white throat marking in an aggressive posture, and the concealment of same in a submissive posture, conform to the observation of Watson and Jenkins (1964) and Lumsden (1968) that these structures may be important indicators and releasers of aggressive behaviour.

The postures in photographs interpreted by MacDonald (1968: Fig. 10 and 11), and subsequently Hjorth (1970: Fig. 31), as positions characteristic of threatening male Franklin's Grouse were never observed in this study. As they involve a number of components from various behaviour patterns and were elicited by mirror props in the presence of a female dummy, these attitudes likely represent non-stereotyped conflict behaviour involving escape, threat, and sexual tendencies.

The "Oblique" (Hjorth 1970: 243) was very rarely seen and only in response to the close proximity of a human by a non-habituated male in a tree in spring. It appears to be a posture exhibiting conflict behaviour with high escape tendencies, because of the exposed leading edges of the wings.

The failure to note any "hooting" during more than 178

hours of direct observation of males in this study, in addition to the anatomical evidence provided by Hjorth (1970) that male Franklin's Grouse do not possess an inflatable oesophagus or a voluminous syrinx, appear to dispel the surmisals by Stoneberg (1967), MacDonald (in Hjorth 1970), and Johnsgard (1973) that Franklin's Grouse may be capable of uttering "hooting" sounds. Short (1967) on the other hand, reported "small cervical vocal sacs" in the canadensis race, in which Lumsden (1961) had noted a "Hiss-plus-Squeak Call" accompanying the Tail-fannings display. The lack of similar anatomical structures may explain the absence of this "call" from the homologous display of male Franklin's Grouse. The lack of this call, a closed beak during the Pecking Display, and the additional Wing-claps appear to be the primary behavioural differences between C. c. franklinii and other subspecies of Spruce Grouse.

Anderson (1973) and Herzog and Boag (1978) believed the clumped pattern of distribution shown by territorial males was a result of social attraction. The previously mentioned ability of wing-beat display sounds to attract other Franklin's Grouse concur with their conviction. In addition, the frequently observed commencement of advertizing in response to the sounds of advertizing by a neighbouring resident, demonstrate the existence of a social component in the selection of male territories, but quantification will be required for a more complete understanding of this

relationship.

Most previous authors have suggested that the majority of yearling males do not exhibit territorial behaviour, even if they become localized (Ellison 1971; Anderson 1973; Herzog and Boag 1978). However, observations in this study indicated that some yearling males were capable of establishing and defending a territory, through advertizing and threat behaviour that was indistinguishable from that of older territorial males. The majority of yearling males encountered though, displayed subordinance to a threatening male, fled from the area occupied by such a male, and rarely returned to the vicinity. Thus, dominant males, as assessed by status related posturing during intrasexual interactions, tended to remain, while submissive acting males tended to leave the study area. These observations therefore, complement the findings of Herzog and Boag (1978) that yearlings that are unsuccessful in competing for space, are forced to emigrate to non-disputed areas. In addition, they confirm the suggestion of Alway and Boag (1979) that aggressive behaviour on the part of dominant territorial residents appears to be responsible for the dispersal of yearlings in spring. More specifically, it appears that dominant males may recruit to the population at a greater rate than submissive males. The factors which determine why some yearling individuals emigrate from a population, and why others appear to possess sufficient status to stay, are unclear and require further research.

When the restrictions on entry to a fixed area exclude conspecifics of one or more castes, or involve appeasement or submissive behaviour by intruders over the whole or part of the area, there is evidence of a form of territorial behaviour (McBride 1976). This was evident in observations of male Franklin's Grouse. Aggressive interactions seem to be occasionally required to establish ownership over disputed space, either with intruding yearling males or neighbouring residents. Territorial males in the breeding season were never encountered on the territory of another, only in threat interactions with intruders or adjacent territorial males along presumed territory boundaries. It is obvious then, that the breeding territories of male Franklin's Grouse, like those of females (Nugent 1979), conform to the concept of a "defended area" (Brown 1969), and that this defense is accomplished by territorial behaviour. It appears that territorial males are spaced by mutual avoidance of areas occupied by other advertizing males. Through threat behaviour, territorial neighbours appear to form relationships which determine where each shall move, and through advertizing behaviour each seems to be able to monitor the presence and whereabouts of the other. A similar means of spacing was evidenced among females in spring (Nugent 1979).

Table 1. Behaviour terminology (text), authority, and abbreviations (tables and figures).

Behaviour	Authority	Term Used In Text	Abbreviation
Male aggressive call	MacDonald 1968	aggressive call	AgC
attentive-Upright	———	Upright	aUpr
Circling cum Strutting	———	Circling	CS
Driving Flight	———	Driving Flight	DF
Stationary Wing Drums	Hjorth 1970:242	Drums	DR
Forward Arcing cum Aggressive Calling	———	Forward Arcing	FA
Flutter Flight	Hjorth 1970:242	Flutter Flight	FF
Forward Rush	———	Forward Rush	FR
Fight	———	Fight	Ft
other behaviour observed in advertizing bouts	———	other advertizing	Oa
other behaviour observed in threat interactions	———	other threat	Ot
Pecking Display	———	Pecking Display	PD
Rush cum Homestacy Tail-fannings	Hjorth 1970:246	Tail-fannings	RcTf
Tail-flicking	———	Tail-flicking	Tfk
moving toward-Display walking cum Tail-swaying	———	Tail-swaying	TSw
Flutter Flight cum Wing-claps	Hjorth 1970:242	Wing-claps	WC

Table 2. Hourly and seasonal movements and frequencies of male Franklin's Grouse advertizing and threat behaviour in spring and early summer.

Time Interval (MST)	Season	Minutes of Observation	Advertizing Behaviour (%/hr.)*	Threat Behaviour among males Type A (%/hr.)*	Type B (%/hr.)*	Mean Hourly Flight Movement (m)	Mean Hourly Number Flights	Mean Total Hourly Movement (m)
DAWN (0300-0500)	spring	315	44.1	0	0	84.3	14.2	99.0
	early summer	505	7.6	0	0	16.9	1.8	19.1
EARLY MORNING (0500-0900)	spring	1277	25.8	7.1	0	47.3	4.3	116.0
	early summer	810	3.4	0	0	2.8	1.0	16.2
DAY (0900-1600)	spring	1728.5	1.0	0	0	12.7	0.9	54.0
	early summer	1257	3.8	0	0.4	2.9	0.7	44.7
EVENING (1600-2000)	spring	2408	20.1	4.9	0	32.2	6.3	86.5
	early summer	1339	5.1	1.4	33.0	18.2	2.0	32.7
DUSK (2000-2200)	spring	800	30.4	2.7	0	91.1	6.2	118.3
	early summer	285	24.7	0.1	0	67.0	5.0	75.1

* %/hr. was calculated from the total observation time during the designated time interval of each season.

Table 3. Differences between male Franklin's Grouse advertizing and threat behaviour. See Table 1 for behaviour names.

Characteristic	Advertizing	Threat
seasonal frequency (hrs./100 daylight hrs.)		
spring (n=108.8 hrs.)	20.8	3.97
early summer (n= 69.9 hrs.)	6.6	0.49
most frequent period of day	dawn, dusk, early morning, evening	early morning, evening
mean bout duration (min.)	57.8 (n=10)	21.2 (n=14)
most frequent acts	aUpr, FF, Dr, WC (n=672 acts)	aUpr, TSw, PD, AgC, RcTf (n=376 acts)
diagnostic acts	FF, WC, Dr (n=672 acts)	PD, AgC, RcTf, FA, FR, DF (n=376 acts)
% time on ground	38.1 (n=1067.5 min.)	84.9 (n=263 min.)
% time stationary	78.3 (n=345 min.)	96.2 (n=197.5 min.)
mean absolute movement / bout (m)	fly 153.2 + walk 40.6 (n=10)	fly 38.4 + walk 71.3 (n=14)
mean no. flights / bout	25.5	2.1
% movement by flight	79	35
mean rate movement (m / hr.)	fly 159.9 + walk 42.1 (n=570.5 min.)	fly 113.3 + walk 211.5 (n=197.5 min.)

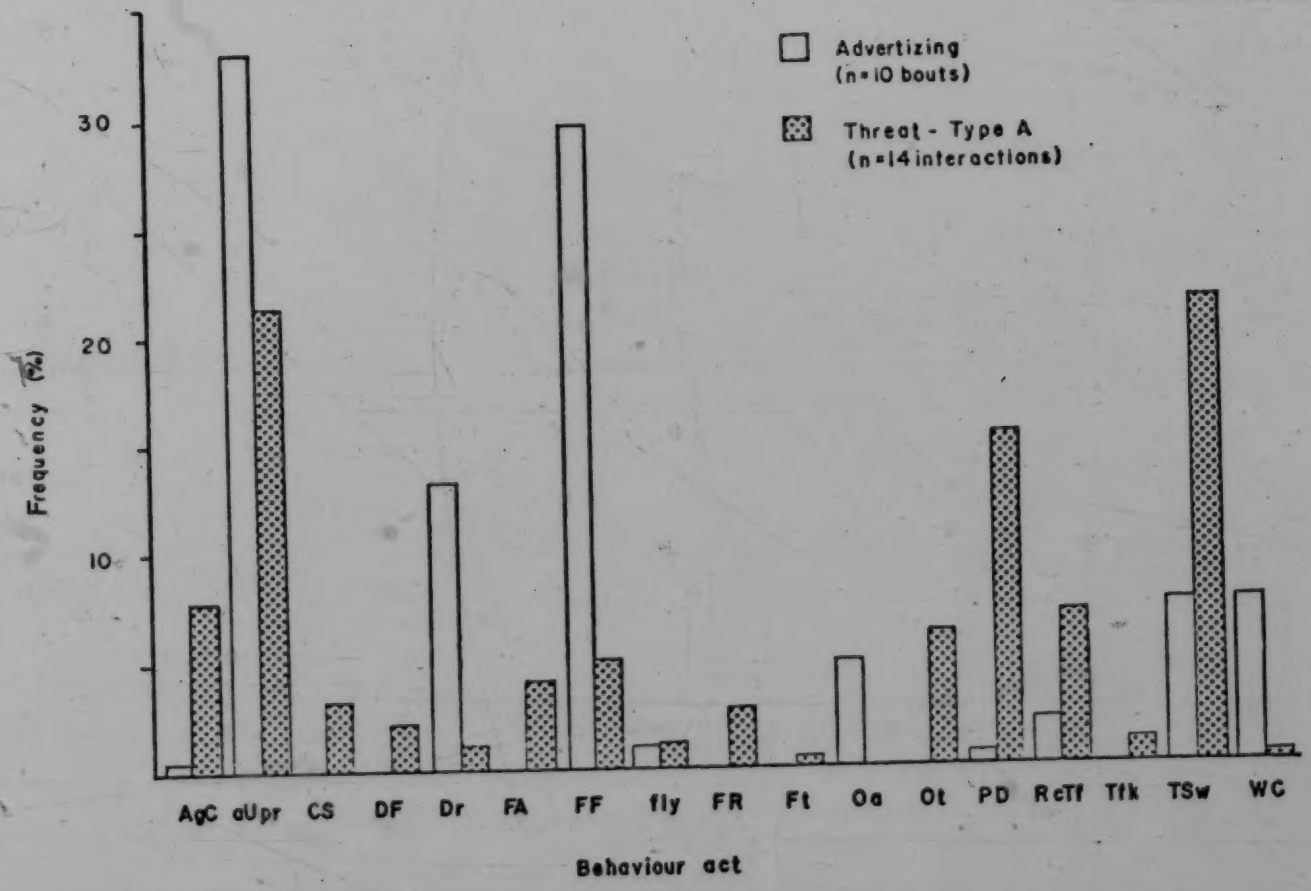
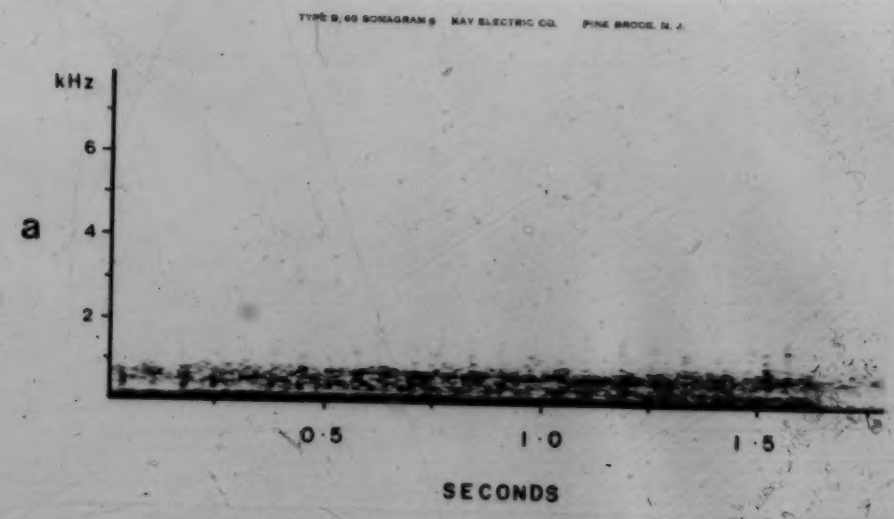


Figure 1. Frequencies of behaviour acts (arranged alphabetically) involved in male Franklin's Grouse advertizing and threat. See Table 1 for behaviour names.

Figure 2. Sonograms of vocal and wing-produced sounds of male Franklin's Grouse: a. Flutter Flight; b. Wing-claps; c. aggressive call.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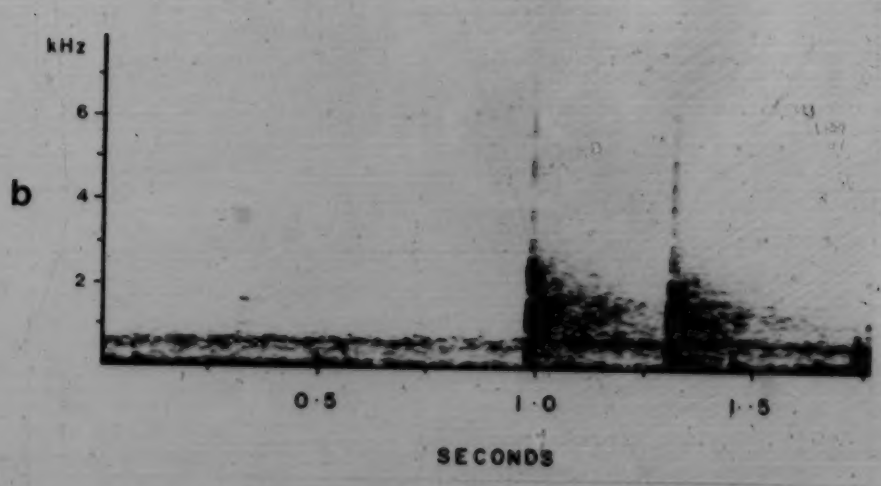
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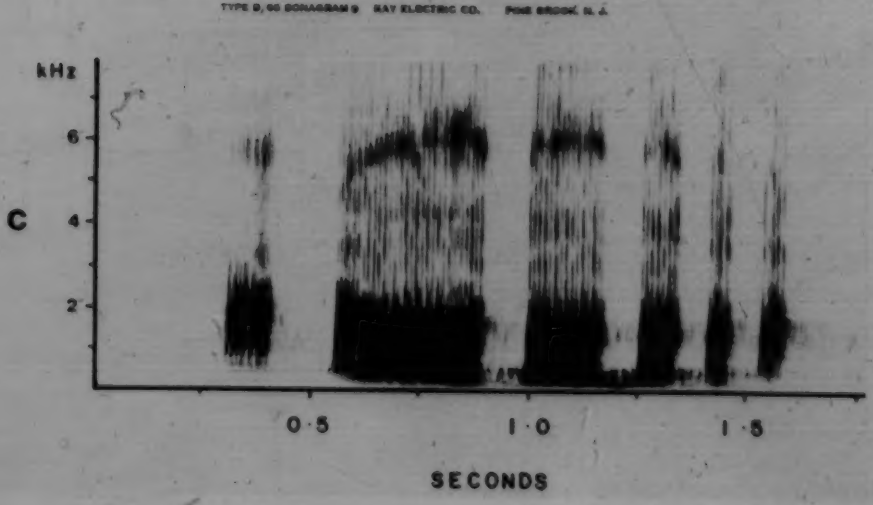
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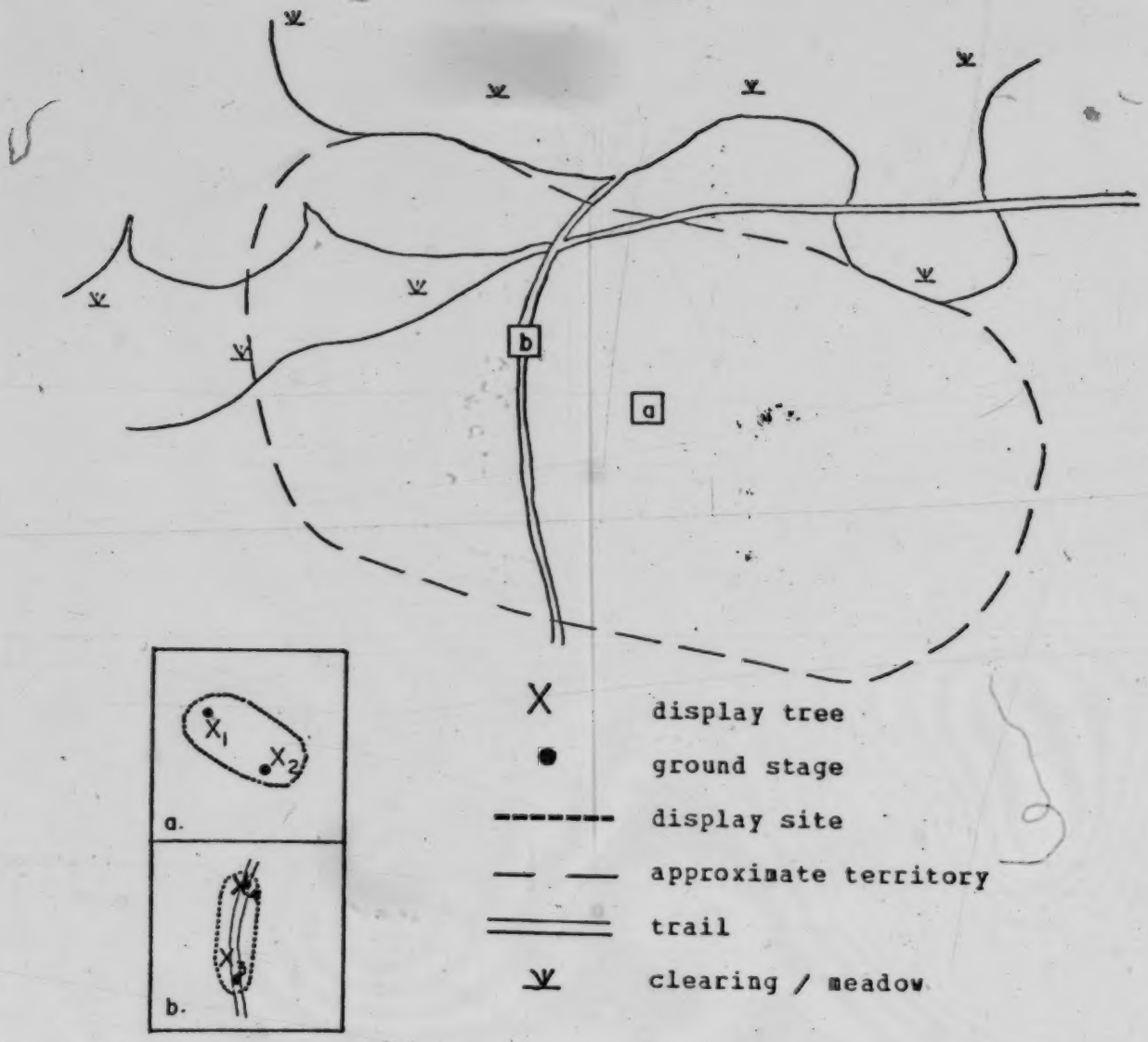

Figure 3. Territory and display sites of a male Franklin's Grouse (scale: 1cm=66m): main display site (a), and secondary display site(b; scale: 1cm=20m).

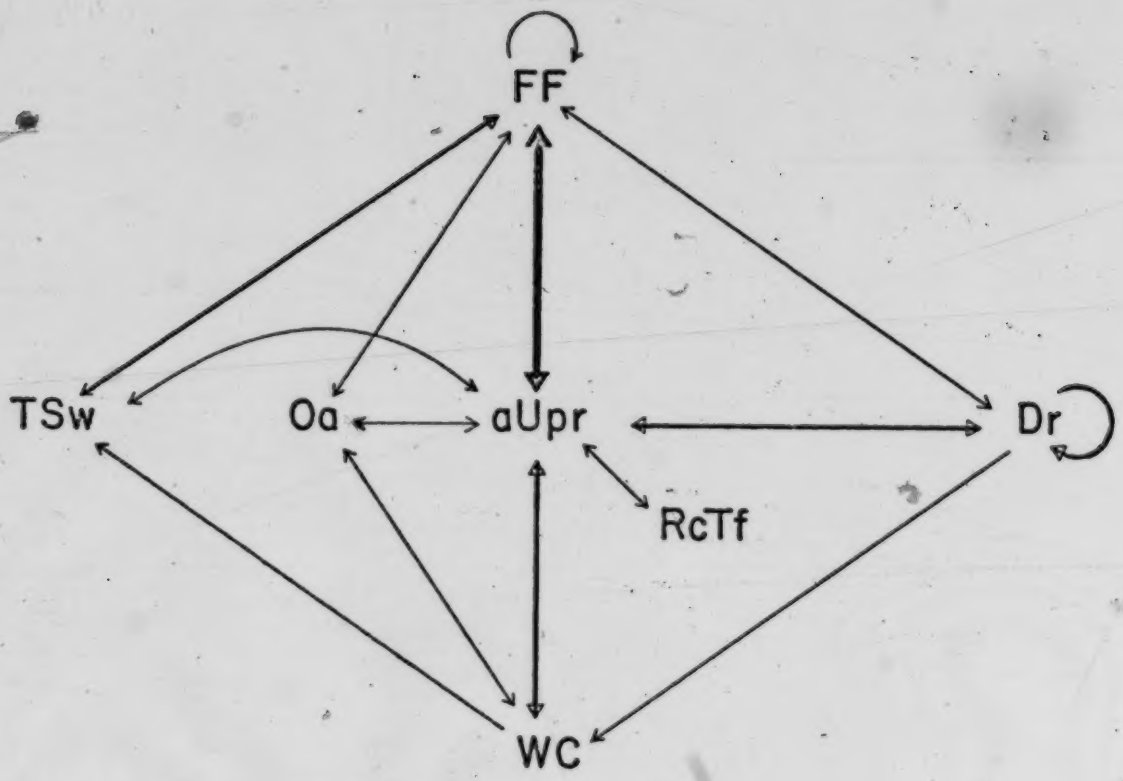

Figure 4. Advertizing sequence of male Franklin's Grouse. See Table 1 for behaviour names.

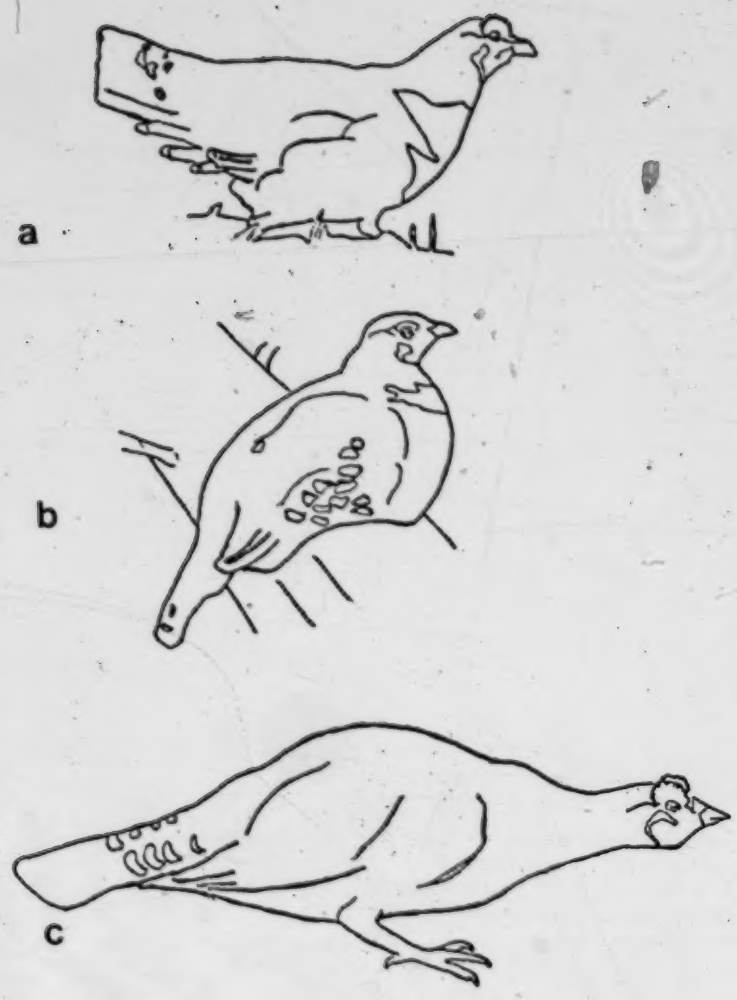

Figure 5. Agonistic postures of male Franklin's Grouse (based on 35 mm photographs): a. Forward Arcing; b. submission; c. Forward Rush.

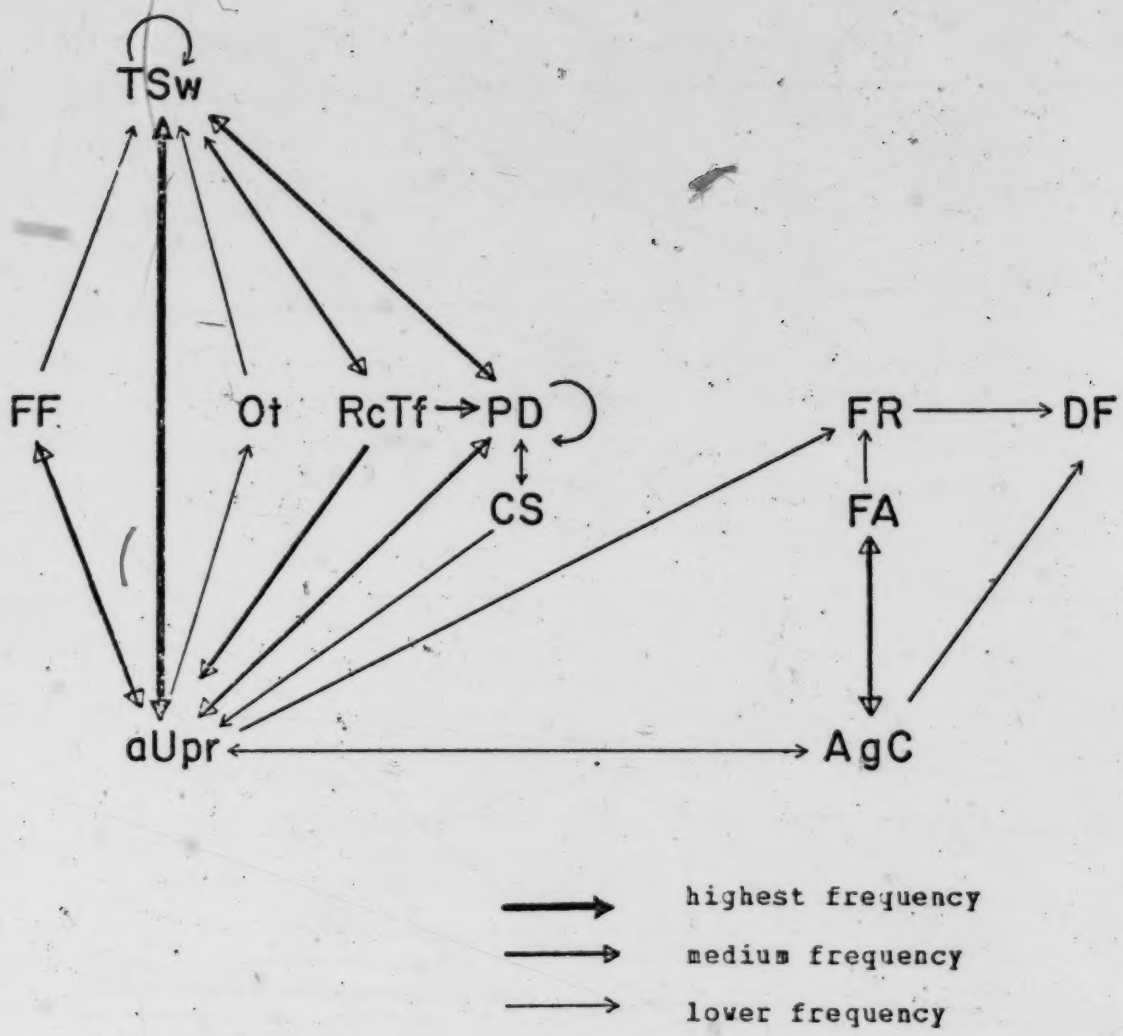

Figure 6. Threat behaviour (Type A) sequence of male Franklin's Grouse. See Table 1 for behaviour names.

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APPENDIX 1: Frequency distribution of male Franklin's Grouse two-act advertizing sequences. Each row corresponds to the initial act in a sequence, and each column to the successive act.

Initial act \ Following act	AgC	aUpr	Dr	FF	fly	Oa	PD	RcTf	TSw	WC
AgC	0	2	0	0	0	1	0	0	1	0
aUpr	3	6	41	112	6	7	1	6	11	36
Dr	0	30	27	21	0	2	0	0	0	8
FF	0	137	12	12	0	9	0	6	21	0
fly	0	2	0	0	0	4	0	0	0	0
Oa	1	8	3	12	1	1	0	0	2	5
PD	0	0	0	0	0	0	0	0	1	2
RcTf	0	10	1	0	0	0	1	0	0	0
TSw	0	4	3	37	0	3	1	1	0	0
WC	0	27	2	4	0	5	0	0	13	0

APPENDIX 2: Frequency distribution of male Franklin's Grouse two-act threat behaviour sequences.

Initial act \ Following act	AgC	aUpr	CS	DF	Dr	FA	FF	fly	FR	Ft	Ot	PD	ReTf	Tfk	TSw	WC
AgC	32	4	1	3	1	13	0	0	1	0	1	1	0	2	0	0
aUpr	4	0	3	0	2	0	10	4	2	0	6	13	1	0	36	0
CS	1	3	1	0	0	0	0	0	1	0	0	2	1	2	0	0
DF	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Dr	0	1	0	0	0	0	2	0	0	0	1	0	0	0	0	0
FA	14	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
FF	1	8	0	0	0	0	2	0	1	0	2	1	1	0	5	0
fly	0	3	0	0	0	0	0	0	1	0	0	0	0	0	0	0
FR	0	1	1	2	0	0	2	0	0	1	1	0	1	0	0	0
Ft	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Ot	0	4	0	0	0	0	1	0	1	0	5	3	2	0	7	0
PD	2	15	4	0	1	0	1	0	1	0	2	17	0	1	16	1
ReTf	1	11	0	0	0	0	0	0	0	0	0	9	0	0	5	0
Tfk	2	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0
TSw	1	30	1	2	0	1	1	0	0	0	4	12	20	0	10	0
WC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0

CONCLUDING DISCUSSION

Resident male and female Franklin's Grouse apparently maintained and defended their respective territories throughout most of the breeding season. Occupancy of such a space was advertized by wing-produced acoustic signals broadcast at large. Females additionally advertized with a form of song - the Cantus - primarily just before and during laying. Defense of respective territories against intrusion by conspecifics involved threat behaviour, that was relatively stereotyped among territorial males, but not as evident among females. Threat behaviour during interactions between contiguous territorial residents and trespassing conspecifics, was accompanied by vocal signalling in both resident males (aggressive calls) and females (Cantus).

Sonographic analysis of Franklin's Grouse flight signals and the Cantus of females indicated that the acoustical characteristics of these sounds appear to be adaptive for communicating in the dense pine foothill forests inhabited by these grouse (Hooker 1968; Morton 1975; Hjorth 1976; Wiley and Richards 1978). The temporal resolution of acoustic signals found in other avian species (Schwartzkopff 1968; Wilkinson and Howe 1975), suggests that if grouse have similar capabilities, they may be able to discriminate individual differences, or at least identify the sex of an unseen grouse from its flight sound. This ability seemed apparent in field observations of Franklin's Grouse, and is thought to be advantageous to territorial

birds for detecting potential mates or intruders.

Through acoustical and optical signalling in advertizing and threat behaviour during the breeding season, territorial Franklin's Grouse seemed to have evolved a system of communication whereby they can monitor the whereabouts of each other. By mutual intrasexual avoidance of areas occupied by other advertizing individuals, territorial birds appear to have formed local relationships which, through this spacing, appear to allow a division of the ecological resources.

Yearlings appeared to emigrate from an area in spring primarily in response to social aggression encountered from resident territorial birds. An undisputed space in the vicinity of the brood or winter range would not exist if already occupied by a resident. Less aggressive individuals appeared to move away from areas where the potential for social aggression was high, to other areas which may be less suitable. This hypothesis is supported by personal observation and data from Boag et al. (in prep.), who found that the number of juveniles recruited was negatively correlated with the number of adults in an area. These movements are therefore considered to be a result of spacing behaviour (Alway and Boag 1979).

However, a sufficiently high level of dominance seems to preclude the necessity for some juveniles to disperse. For example, a young male observed over two years, established on the home range of its female parent during

its first winter. The previous resident adult male of this territory was never sighted again. It is not known whether the young male displaced the adult, but is presumed, as this yearling was a particularly aggressive individual which would approach and vocally threaten even human territorial intruders, not only in the spring territorial season, but also in summer and fall to a lesser degree. This yearling exhibited advertizing and threat behaviour indistinguishable from that of older males. At least one brood originated in the vicinity of this male. No other territorial males were encountered in the immediate area. The behaviour of this male indicated that a high degree of aggression and display competence may be sufficient to allow some yearling males to establish, maintain, and defend a territory, and to compete with adult males for the attentions of a female(s).

The observed apparently high level of intrasexual social intolerance and aggression shown by laying and early incubating females seems adaptive in achieving wide dispersion of nests. The high vulnerability to predation in the egg stage, observed in this study and others (Keppie 1975; Herzog 1977), may have been an effective selective pressure for the evolution of maximal nest dispersion (cf. Lack 1968). However, as aggressive interactions between resident females during this relatively critical bioenergetic phase (Kendeigh 1973; King 1973) were as aggressively reciprocated, and often apparently spontaneous, and involved considerable expenditure of energy both in

travel and interaction, there is probably a social component involved that has not been adequately examined. This social interaction may be important in regulating the population by determining the annual production in a density dependant manner. The greater the density of females, the greater would be the frequency of agonistic encounters between territorial females. Strife through territorial interactions may thus sufficiently psychologically stress the less dominant females from normal laying and nesting practice to decrease overall annual production. Frequent agonistic encounters are felt to affect the physiology of a population through the pituitary-adrenal-gonadal axis (Carrick 1963; Calhoun 1964; Christian 1971; King 1973). Physiologically stressed individuals may readily succumb to resource shortages, predation or severe weather, or fail to mature and reproduce (op.cit.). In addition, dominant females of other grouse species have been observed to delay or completely inhibit production in subordinate females (Kruijt and Hogan 1967; Lumsden 1968; Silvy 1968; Robel 1970; Watson and Moss 1971; Robel and Ballard 1974; Hannon 1978). Boag et al. (in prep.) found an inverse relationship between the density of Franklin's Grouse in the spring and the production of juveniles per individual in that population, which may be indicative of such a relationship. Zwickel (1975) and Bowen (1971) documented negative correlations between clutch size and nest establishment date in Blue Grouse and Greater Prairie Chicken, Tympanuchus cupido.

Therefore, any delay in the mating of other females by a mated (laying) female has the potential of reducing the number and size of successful clutches in the population.

The function of intrasexual aggression among female Franklin's Grouse may be two-fold. Early in the spring, a rise in aggression among females in a local population appears to space individual females on territories. Those unsuccessful in acquiring a territory appear to be forced out of the immediate area. This spacing appears to produce maximal nest dispersion. Further aggression among resident females may determine the relative proportion of the female population that will be successful in producing a clutch.

Male intrasexual aggression similarly is expressed in territoriality which appears to have been selected to ensure that the majority of breeding is accomplished by the presumed "most fit" (ie. territorial) males in relation to the population density. Localization of such males by territoriality seems to allow territorial (presumably the "most fit") females to monopolize access to such males and/or the resources on their territories. This hypothesis is supported by observations of all resident males interacting only with the resident female whose territory overlapped that of the male (n=700+ hrs observ.).

Franklin's Grouse territorial behaviour may therefore be influencing the reproduction rate of the population at "critical density level 2 " (Brown 1969). However, the full importance of territorial behaviour in regulating

populations remains to be demonstrated on populations with different levels of density (op.cit.).

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